National Library of Canada
Acquisitions and Bibliographic Services Branch
395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale du Canada
Direction des acquisitions et des services bibliographiques
395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

UNIVERSITY OF ALBERTA

RANGE ECOLOGY OF AN INTRODUCED REINDEER POPULATION ON THE BELCHER ISLANDS, NORTHWEST TERRITORIES, CANADA.

BY

JOHN S. NISHI

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of Master of Science.

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta

Fall 1993

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file *Votre référence*

Our file *Notre référence*

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-88422-3

Canada

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: JOHN S. NISHI

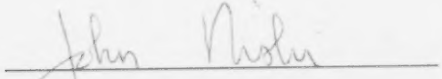
TITLE OF THESIS: RANGE ECOLOGY OF AN INTRODUCED REINDEER POPULATION ON THE BELCHER ISLANDS, NORTHWEST TERRITORIES, CANADA

DEGREE: MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED: FALL 1993

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as hereinbefore provided neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.



10921 University Avenue
Edmonton, Alberta.
T6G 1Y1

DATE: 7 OCTOBER 1993

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled RANGE ECOLOGY OF AN INTRODUCED REINDEER POPULATION ON THE BELCHER ISLANDS, NORTHWEST TERRITORIES, CANADA submitted by JOHN SUSUMU NISHI in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

S.A. Boutin (Co-Supervisor)

G.H.R. Henry (Co-Supervisor)

R.J. Hudson

J. Roland

Date: 7 October 1993

Abstract

Caribou (*Rangifer tarandus caribou)* once inhabited the Belcher Islands of southeast Hudson Bay, but disappeared in the 1800's. In March 1978, 60 reindeer *(R. t. tarandus)* were introduced to the Belcher Islands. Since their introduction, the reindeer population has increased rapidly. Currently there are over 561 animals which occur principally in southern Flaherty Island. In this study, my objectives were twofold. Firstly, I described important range communities and assessed the impact of grazing by reindeer on vegetation. I sampled range communities from areas with different relative densities of reindeer. Counts of pellet groups within transects were used to quantify relative use by reindeer. Grazing intensity (as indicated by pellet-group densities) had a significant effect on plant abundance. Lichens, and grasses and forbs decreased significantly as grazing intensity increased. Conversely, cover of bare soil and litter was significantly greater at heavily grazed stands compared to moderately grazed and ungrazed stands. I conclude that reindeer have overgrazed lichen-dominated range in southwest Flaherty Island. In addition, intense and repeated browsing of willows *(Salix glauca* and *S. lanata)* by reindeer has likely hastened mortality of those shrubs in southwest Flaherty. This observation is important because willows are a species generally known for their high rates of growth and ability to withstand brief episodes of intensive browsing. Secondly, I described seasonal range use and diets, and body composition of reindeer in late winter to determine whether forage availability may be limiting. I assessed range use from pellet-count data, and analyzed rumen and fecal samples to determine winter and summer diets. Winter type pellet-groups were most abundant in lichen-dominated range, whereas summer type pellets were most abundant in both lichen and willow-dominated range communities. Diet analysis confirmed the importance of lichens and willows to reindeer; lichens accounted for greater than 50% of rumen contents in winter whereas willows represented over 97% of summer fecal pellets. Despite localized overgrazing, Belcher Island reindeer are comparatively large with respect to genetically related reindeer in North America. Large body size and rapid growth rates of individuals are expected when ungulates are introduced to a new environment where per capita food availability is high. Adult female reindeer still had excess fat reserves in late winter suggesting that food availability was not limiting. These results show that there is a lag between the time that lichens are overgrazed and the time that reindeer become negatively affected.

Acknowledgments

The 'North' is a long way from home for a farm boy from Southern Alberta. However, field experiences on the Belcher Islands have been some of my most challenging and rewarding.

To my parents, Saburo and Kimino, you are the hardest working people that I know of; thank-you for your love and support in a career that will take me away from the farm. To my sisters, especially Audrey who had to put up with my life as a graduate student, thank-you for your patience and understanding. To my great friends Shawn, Brad, Sue, Yves, Rick, and Hilary, you helped me keep perspective throughout my program, for that I am always grateful.

A warm hello and handshake to the many smiling faces in Sanikiluaq and all the members of the Weasels' Hunters and Trappers Association. The HTA provided all logistic support in the field, and safely moved us from site to site. I hope that this thesis will be useful in discussing future management plans for the reindeer. L. Arragutainaq (Sr.) coordinated our ferry trips and was an excellent translator at HTA meetings. B. and M. Fleming welcomed me with their warm hospitality and made their little pink house my "Arctic Home."

In the field it is especially true that you are only as good as the people around you. I would not have been able to conduct this study without the dedicated assistance and enthusiasm of Y. Pinsonneault and L. Arragutainaq (Jr.). I will miss Lucassie - my friend and field assistant for two summers - may you rest in peace.

F. Miller and D. Thomas provided helpful comments and suggestions on drafts of my proposal. J. Edmonds generously lent me her maps and satellite photos. P. Marceau and M. Meeko provided guidance in the lab. B. Nicholson, S. Vitt, and C. Young willingly shared their expertise on the TWINSPAN and CANOCO software packages. And finally, I thank my supervisory committee, S. Boutin, G. Henry, R. Hudson, and J. Roland for their support and helpful suggestions and comments. A special thanks to G. Henry who gave me more than one opportunity to work in the Arctic.

Operating funds for this study were provided by the Weasels' Hunters and Trappers Association, Canadian Wildlife Service, Canadian Circumpolar Institute, Department of Indian and Northern Affairs, and the Northern Student Training Grant. I gratefully acknowledge funding from the Department of Zoology, the Province of Alberta (Graduate Scholarship), and the Beverly and Kaminuriak Management Board (Scholarship).

Table of Contents

Abstract .....

Acknowledgments .....

List of Tables .....

List of Figures .....

Chapter 1. General Introduction 1

Chapter 2. Long-term effects of grazing by reindeer on vegetation 6

Chapter 3. Seasonal range use and diets, and late winter body condition of an increasing population of reindeer 49

Chapter 4. General Discussion 79

Appendix 1. Climatic data at Inukjuak and Kuujjuarapik, Quebec 85

Appendix 2. Snow surveys on the Belcher Islands 87

List of Tables

Table ..... **Page**

Table 2-1. Relationship between ground cover (per cent) and aboveground standing crop (g/m^2) of different plant growth forms. 29

Table 2-2. Cover values for vegetation within five community-types as delimited by TWINSPAN (see Figure 2-2). Species and stands are arranged in an ordered two-way table (Hill 1979). 30

Table 2-3. Summary of ordination analyses for lichen-dominated range communities on the Belcher Islands. The first axis is constrained to measured environmental variables (redundancy analysis), whereas the second, third, and fourth axes are unconstrained (principal components analysis).
A) First axis constrained to all measured environmental variables. 32
B) First axis constrained to pellet-group densities only (*via* forward selection of environmental variables). 32

Table 2-4. Mean (± SE) standing crop of vegetation (g/m^2) at eight stands sampled on the Belcher Islands. 33

Table 2-5. Mean biomass allocation (% of total weight ± SE) in shoots of *Salix glauca* and *S. lanata* in stands with different intensities of use by reindeer. 35

Table 2-6. Nutritional characteristics of current growth in shoots of *Salix glauca* in stands with different intensities of use by reindeer. 36

Table 2-7. Nutritional characteristics of current growth in shoots of *Salix lanata* in stands with different intensities of use by reindeer. 37

Table 3-1. Average number of reindeer pellet-groups (± standard deviation) counted within belt transects (2m x 100m) on the Belcher Islands. Sample sizes are presented in parentheses. 64

Table 3-2. Pairwise comparisons of observed pellet-group distributions from four base camps using Kolmogorov-Smirnov two sample tests. 65

Table 3-3. Composition of summer diet of Belcher Island reindeer. The micro-histological technique (Sparks and Malechek 1968) was used to estimate mean percent relative density (± SD) of plant cuticular fragments in fecal samples composited by year. Means based on four slides of 20 fields each. 66

Table 3-4. Composition of rumens collected from Belcher Island reindeer in late winter. The point estimate technique (Chamrad and Box 1964) was used to estimate mean proportion (±SE) of plant fragments retained on a 2 mm sieve for each rumen sample. The micro-histological technique (Sparks and Malechek 1968) was used to estimate mean percent relative density (± SD) of plant cuticular fragments in rumen samples

composited by year. Means based on four slides of 20 fields each. 67

Table 3-5. Percentage of lichens and shrubs identified using the point estimate technique on rumen contents collected in late winter. 68

Table 3-6. Nutritive quality (% ± SE) of washed rumen contents of reindeer collected on the Belcher Islands, Northwest Territories. 69

Table 3-7. Liveweights and indices of body condition for Belcher Island reindeer in March (1989-1991). Means are presented with standard errors; sample sizes in brackets. 70

Table 3-8. Average weight of adult female reindeer on the Belcher Islands and comparative data from other reindeer herds in North America and Russia. 71

List of Figures

Figure ..... **Page**

Figure 2-1. Locations of field camps on the Belcher Islands, Northwest Territories. Camps established in 1990 are represented by integers, and letters denote camp locations in 1991. 38

Figure 2-2. Dendrogram of TWINSPAN classification for stands of vegetation sampled on the Belcher Islands. Indicator species are shown on the right or left hand side of the dichotomy; integers in brackets indicate cover values on a scale of 1 to 5 using the following categories based on average cover values within a stand: 1, 0.01 - 1.9%; 2, 2 - 4.9%; 3, 5 - 9.9%; 4, 10 - 19.9%, 5, 20 - 100%. Eigenvalues are presented in brackets below each branch. Descriptions of community-types are based on Edmonds' (1979) range study. 39

Figure 2-3. Typical caternary sequence of range communities on the Belcher Islands as related to elevation and moisture regime. 40

Figure 2-4. Comparative analysis of ground cover of plant growth forms in ungrazed (white bars) (n = 4), grazed (cross-hashed) (n = 4), and heavily grazed (black bars) (n = 5) stands in the mixed lichen - dwarf shrub range type. Bars indicate mean cover values (± SE). Different letters within a growth form indicate significant differences ($p < 0.05$). 41

Figure 2-5. Ordination diagram based on a hybrid of redundancy analysis and principal components analysis on the floral composition of 13 stands in lichen-dominated range communities (community-type A; see Table 2-2 and Figure 2-2) on the Belcher Islands. The first axis is constrained by densities of reindeer pellet groups in a stand. The second axis displays residual variation in species composition of lichen-dominated communities, *i.e.*, variation not explained by pellet group densities. Species are represented by arrows and abbreviations are as follows: Ale och, *Alectoria ochroleuca*; Bry div, *Bryocaulon divergens*; Cet cuc, *Cetraria cucullata;* Cet niv, *C. nivalis;* Cet isl, *C. islandica;* Cla mit, *Cladina mitis;* Cla ran, *C. rangiferina;* Epi lat, *Epilobium latifolium;* Lat jap, *Lathyrus japonicus;* Pyr gra, *Pyrola grandiflora;* Sax tri, *Saxifraga tricuspidata;* Dry int, *Dryas integrifolia;* Emp nig, *Empetrum nigrum;* Rho lap, *Rhododendron lapponicum;* Sal gla, *Salix glauca;* Sal ret, *S. reticulata;* Vac uli, *Vaccinium uliginosum;* Vac vit, *V. vitis-idaea.* Stands are represented by solid squares and abbreviations are as follows: U, ungrazed; G, grazed, and H, heavily grazed; numbers or letters in brackets denotes location of base camp (see Figure 2.1). ($\lambda_1 = 0.30$, $\lambda_2 = 0.25$, scaling: 1 for species, and 1.75 for sites). For summary statistics see Table 2-3B. 42

Figure 3-1. A) Population counts of reindeer introduced to the Belcher Islands, Northwest Territories, 1978 - 90 (data from Ferguson (1985) and Arragutainaq *et al.* (1990)). The original herd was introduced in March 1978 and consisted of 50 adult females and 10 adult males. 72

B) Observed rate of increase of reindeer. The curve was constrained to pass through the number of animals introduced in 1978 ($y = 4.09 + 0.20 x$, $r^2 = 0.95$, $p = 0.005$; where x is years since introduction). .. 72

Figure 3-2. Average densities of reindeer pellet-groups in different range communities on the Belcher Islands. Bars represent the upper 95% confidence limit of the mean. In the legend, "Summer" and "Winter" refer to the classification of pellet-groups; summer type pellets were an amorphous mass of several individual pellets whereas winter pellets were hard and spherical. Data from Camps A and C, and Camps B and D were pooled into "Low use" and "High use" groups respectively (see Analyses). 73

Chapter 1

General Introduction

History of caribou and reindeer on the Belcher Islands

Caribou *(Rangifer tarandus caribou)* once inhabited the Belcher Islands of southeast Hudson Bay, but they disappeared sometime during 1840-50 (Elton 1965), or in the late 1870's (Flaherty 1918). Local Inuit suggested that extinction of caribou from the Belchers was caused by severe icing conditions that resulted in mass starvation (Elton 1965, Flaherty 1918). Alternatively, caribou may have migrated from the Belchers to mainland Quebec (Elton 1965). In the high arctic, inter-island movements have been documented for Peary caribou *(R.t. pearyi)* and proposed explanations for those movements are range degradation caused by an expanding population or restriction of access to forage as a result of snow/ice conditions (Miller *et al.* 1977).

Since the extinction of the caribou population, there were no large herbivores on the Belcher Islands. At the request of Belcher Island Inuit, the Government of the Northwest Territories (GNWT) purchased 60 reindeer (*R. t. tarandus*) from the Mackenzie Delta herd and released them on the Belchers in March 1978. The GNWT selected reindeer as opposed to capturing and transporting wild caribou because reindeer were cheaper to obtain, easier to handle, and would probably not disperse from the Belcher Islands (Anonymous 1983). Since its introduction, the reindeer population has grown rapidly and recent surveys indicate that there are at least 561 reindeer on the Belchers (Arragutainaq *et al.* 1990). In January 1983, a limited harvest of reindeer was initiated by Inuit (Ferguson 1985).

In Canada, reindeer are considered domestic livestock because they are not indigenous to North America (Anonymous 1982). Thus, Belcher Island Inuit own the reindeer and are responsible for management of the population. Consequently, there was a local concern regarding the long term harvest and health of reindeer because there was no real management plan in place. In 1987, on behalf of the community of Sanikiluaq, the Weasels' Hunters and Trappers Association (HTA) approached researchers at the Canadian Circumpolar Institute (University of Alberta) to assist them in developing a community-based management strategy that would incorporate both local knowledge and expertise, and the outside assistance and skills of research scientists.

Fundamental to management of the reindeer population was an assessment of range communities and the potential impact of reindeer on vegetation. A preliminary assessment of range on the Belcher Islands was conducted in 1978 (Edmonds 1979). From aerial photographs and one month of ground truthing (restricted to the northernmost part of Flaherty Island), Edmonds identified 7 range types. She concluded that summer range was adequate, but that winter range was only fair to good (Edmonds 1979). However, no further studies had been conducted. Thus, this study arose from the need to better understand the relationship between introduced reindeer and their habitat on the Belcher Islands.

Introductions of *Rangifer* to Islands

When an animal population is introduced to a new environment where food is abundant, the population increases rapidly until it exceeds the initial "carrying capacity" (see Macnab 1989) of the habitat. The subsequent reduction in food abundance caused by overgrazing results in an abrupt decline in animal numbers. As animal densities decline, forage plants are able to recover. Finally, animal numbers stabilize with the new level of food abundance. This relationship between an herbivore and its food supply is termed an irruptive oscillation and was originally hypothesized by Riney (1964). An irruptive oscillation is not limited to introduced populations, rather the important prerequisite is a sudden and large difference between animal numbers and available food. Irruptive oscillations are ecological occurrences that are well documented in the literature for a variety of species (Caughley 1970, Sinclair and Norton-Griffiths 1979).

Introductions of reindeer to islands have resulted in variable results (see review by Leader-Williams 1988). Classic examples of irruptive growth followed by crash of the population are well documented (Scheffer 1951, Klein 1968, and see Swanson and Barker 1990). Successful introductions of *Rangifer* to islands seem to be contingent on animals relying on vascular plants, such as graminoids, as their main winter forage as opposed to slow-growing lichens (Leader-Williams 1988). A forage resource with a direct compensatory response to grazing allows herbivore densities to be more closely cued to annual plant production, a requirement for long term stability of herbivore numbers (Caughley and Lawton 1981). Since lichens may require 20 - 40 years for complete recovery (Palmer and Rouse 1945), overgrazing by an expanding reindeer / caribou population can result in a sudden reduction in the amount of available food. Compounded by winter snow or icing conditions, overgrazing of lichens may predispose a population to mass starvation (Klein 1968).

Study objectives

In this thesis, I present the results of a field study on the reindeer and range of the Belcher Islands; the work is but a snapshot in the dynamic relationship between an introduced herbivore and its habitat. I have summarized my findings in the form of two papers with the following questions and objectives.

Chapter 2: Have introduced reindeer affected range communities? My objective was to describe range communities and assess the impact of grazing on vegetation.

Chapter 3: Have reindeer been affected negatively by limited forage availability? My objective was to describe seasonal range use and diets, and late winter body condition of reindeer. Finally, in a general discussion (Chapter 4), I summarize my major findings and provide a general synthesis in the form of implications and recommendations for management.

Literature Cited

Anonymous, 1982. In the Quebec superior provincial court, district of Montreal, Gratton in Montreal: The Province of Quebec vs G. Hudon. Court transcript of judgment, 25 June, 1982. No. 500-36-044-8911. 7 pp.

Anonymous 1983. Reindeer transplanted to the Belcher Islands 100 years after native caribou disappears. Caribou News. 3 (3): 11

Caughley, G., and J.H. Lawton. 1981. Plant-herbivore systems. pp. 132-166. In: R.M. May, editor. Theoretical Ecology. Sinauer, Sunderland, Massachusetts, USA.

Edmonds, E.J. 1979. A study of reindeer *(Rangifer tarandus tarandus)* range on the Belcher Islands, Northwest Territories. Unpublished report. Canadian Wildlife Service. 37 pp.

Elton, C. 1965. Voles, Mice and Lemmings. Cramer-Weinheim, New York, New York, USA.

Ferguson, M.A.D. 1985. Population status of introduced reindeer on the Belcher Islands, Northwest Territories, in March 1982. Northwest Territories Wildlife Service File Report No. 45. 18 pp.

Flaherty, R.J. 1918. The Belcher Islands of Hudson Bay: their discovery and exploration. The Geographical Review. 6: 433-458.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management. 32: 350-367.

Leader-Williams, N. 1988. Reindeer on South Georgia: The Ecology of an Introduced Population. Cambridge University Press, Cambridge, England.

Macnab, J. 1985. Carrying capacity and related slippery shibboleths. Wildlife Society Bulletin. 13: 403-410.

Messier, F., J. Huot, D. Le Henaff, and S. Luttich. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic. 41: 279-287.

Miller, F.L., R.H. Russell, and A. Gunn. 1977. Interisland movements of Peary caribou *(Rangifer tarandus pearyi)* on western Queen Elizabeth Islands, Arctic Canada. Canadian Journal of Zoology. 55: 1029-1037.

Ouellet, J.P. 1992. Ecology on an introduced caribou population on Southampton Island, N.W.T., Canada. Ph.D. Thesis. University of Alberta. Edmonton, Alberta. 123 pp.

Palmer, L.J. and C.H. Rouse. 1945. Study of the Alaska tundra with reference to its reactions to reindeer and other grazing. U.S. Fish and Wildlife Service Research Report. 10: 48 pp.

Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. IUCN Publications New Series No. 4: 261-273.

Scheffer, V.B. 1951. The rise and fall of a reindeer herd. Scientific Monthly. 73: 356-362.

Sinclair, A.R.E., and M. Norton-Griffiths. 1979. Serengeti, Dynamics of an Ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Swanson, J.D., and M.H.W. Barker. 1992. Assessment of Alaska reindeer populations and range conditions. Rangifer. 12: 33-43.

Chapter 2

Long-term effects of grazing by introduced reindeer on vegetation

Introduction

"Introduced populations of large herbivores, if undisturbed, normally follow a pattern of adjustment to the new environment which consists of a single eruptive (irruptive) oscillation" (Riney 1964). These irruptions are caused by an initially large discrepancy between the carrying capacity (see Macnab 1985) and the number of animals actually present. Upon liberation, an introduced population proceeds through four stages: 1) rapid population increase characterized by low mortality and high fecundity, 2) extensive overgrazing of preferred vegetation communities as the population exceeds its carrying capacity, 3) decline in animal densities in response to reduced carrying capacity, and 4) commencement of relative stability between animal numbers and carrying capacity (Riney 1964, Caughley 1970).

Introductions of reindeer *(Rangifer tarandus)* to island ecosystems have resulted in classic examples of population irruptions (*sensu* Riney 1964, Caughley 1970), followed by associated overgrazing and decline of the population (Scheffer 1951, Klein 1968, Leader Williams 1988, and see Swanson and Barker 1991). Eventual success or failure of an introduction may depend on resilience of forage plants to grazing; response of plants to herbivory is a key factor in the ecology of introduced ungulates. Leader-Williams (1988) reviewed 33 cases where *Rangifer* were introduced to islands and argued that crash of an introduced population was a result of their dependence on lichens as the primary source of winter forage. He attributed relative stability and persistence of reindeer introduced on South Georgia Island to their dependence on tussock grasses *(Poa flabellata)* during winter. Thus, if regulated by food abundance, a herbivore population is more stable through time if its rate of increase is closely cued to annual production of plant biomass (Caughley and Lawton 1981) and the plants have a direct compensatory response to grazing (McNaughton 1983). Since heavily grazed lichen stands may require decades for complete recovery (Palmer and Rouse 1945, Pegau 1970b, Chernov 1985, Klein 1987), extensive overgrazing of lichen communities by an expanding *Rangifer* population can result in a sudden reduction in available winter

forage. Compounded by snow (or icing) conditions in winter, overgrazing of lichens may predispose a population to mass starvation (Klein 1968).

Caribou once inhabited the Belcher Islands of southeast Hudson Bay, but disappeared in the mid to late 1800's possibly as a result of severe icing that caused animals to starve or disperse from the islands to mainland Quebec (Flaherty 1918, Elton 1965). Over a hundred years later in March 1978, at the request of local Inuit, the Government of the Northwest Territories purchased 60 reindeer from the Reindeer Grazing Reserve and introduced them to the Belcher Islands (Anonymous 1983). Following this introduction, the herd increased rapidly; recent surveys suggest that the population is at least 561 animals (Arragutainaq *et al.* 1990). A limited harvest of reindeer was initiated in 1983. In January 1984, a community quota equivalent to 50% of the estimated number of yearlings was approved (Ferguson 1985). Nevertheless, the local Hunter's and Trappers Association was concerned because there was no management plan in place to ensure long term direct harvest numbers. The introduction of reindeer to the Belcher Islands presents a unique opportunity to study the effects of an increasing herbivore population on the vegetation.

This study was designed as both an observational sampling survey to confirm representative range communities as described by Edmonds (1979), and as an analytical sampling survey (see Eberhardt and Thomas 1991) to determine whether introduced reindeer may have caused changes in lichen-dominated range communities and aboveground biomass allocation in willows *(Salix glauca* and *S. lanata).* Specifically, I estimated ground cover of plant species in lichen-dominated range communities and sampled willows to compare aboveground biomass and nutritive values of the current growth between sites heavily used, moderately used, and unused by reindeer.

Study Area

The Belcher Islands are located in the southeast part of Hudson Bay, approximately 110 km off the west coast of Quebec (Figure 2-1). The Belchers are a unique archipelago including the Bakers Dozen and King George Islands, and the four main islands of Kugong (665 km^2), Flaherty (2764 km^2), Weigand (74 km^2), and Tukarak (718 km^2) (Edmonds 1979). Of these four main islands, fresh water lakes account for 21% of total surface area (Edmonds 1979). There are also hundreds of small (<1 km^2) offshore islands scattered throughout the archipelago. Relief is generally low ranging from gradually sloping gravel beaches and eskers to precipitous cliffs 50 to 70 m in elevation. Maximum elevation occurs on Tukarak island and is 100 to 115 m above sea level (Jackson 1960).

Geology

The Belchers are a result of three successive episodes of sedimentation and submarine volcanism that occurred prior to the Hudsonian Orogeny (between 2000 and 1650 million years ago) followed by a fourth episode marked by intrusive gabbro dykes. The depositions resulted in a thick (7000-9000 m) and regular succession of rock formations (strata) known as the Belcher Group (Jackson 1960, Ricketts and Donaldson 1981, Ricketts *et al.* 1982, Ricketts and Donaldson 1989). The Belcher Group consists of 14 stratigraphic units (Ricketts and Donaldson 1981).

The unique shape of the Belcher Islands was a result of isoclinal folding of the Belcher Group during the Hudsonian Orogeny. Compression and folding of the Belcher Group was likely caused by intense rifting and volcanic activity during an ocean opening event (Ricketts and Donaldson 1981). Consequently, surficial geology of the Belchers is complex because of the exposured underlying strata. Over 60% of the land surface is dominated by volcanic flows and pillows (*i.e.* basalts) (Ricketts and Donaldson 1981, Donaldson 1986). Remaining surface area is characterized by outcrops of sedimentary rocks (*i.e.* shales, argillites, siltstones, mudstones, dolostones, cherts, and stromatolites) (Jackson 1960, Ricketts and Donaldson 1981, Ricketts and Donaldson 1989).

Glacial deposits of mud, silt, sand, and gravel are widespread throughout the islands and occur as well sorted beaches. These deposits have been reworked by the wind and sea and are found to within meters of the highest elevations (Jackson 1960).

Climate

Although there are no detailed climatic data for the Belcher Islands, Maxwell's (1986) review of climate in the Hudson and James Bay region provides a general and reliable overview for the Belchers. Maxwell (1986) identifies radiation regime, the cold surface waters (sea ice) of Hudson Bay, physical geography, and upper-air circulation and weather systems as controlling factors of weather on the Belchers. These factors cause the climate to be abnormally cold compared to locations at similar latitude in the northern hemisphere. Consequently, weather on the Belchers is characteristic of the low arctic; summer, spring, and fall are relatively brief and winters are long and cold. Data from nearby coastal stations Inukjuak and Kuujjuarapik are presented in Appendix 1 for comparative purposes. These data should be interpreted in the context that offshore climatic conditions are not identical to coastal conditions (Larouche 1990).

Vegetation

Vegetation on the Belcher Islands is considered low arctic tundra (Edmonds 1979). Investigations on the flora are limited. Wynne and Steer (1943) collected bryophytes on Tukarak Island, but quantitative data on vegetation are limited to Edmonds (1979) study of range communities on Weigand Island and the northern part of Flaherty Island. From aerial photographs and one month of ground truthing, Edmonds (1979) delineated seven distinct range communities. She concluded that summer range for reindeer was adequate and that winter range was only fair to good.

Methods and Materials

I use Thomas and Edmonds' (1984) definition of a range community as a "landscape unit with a characteristic assemblage and cover of plant species or geomorphological surface features." Thus, a range community had similar abundance and distribution of plant species and also represented distinct topographic, and edaphic conditions. I use the term "stand" in the context of a particular sample of a range community. I define "transect" as a means of sampling a stand and "quadrat" as the sampling unit.

Sampling design and data collection

An assessment of range condition or trend requires a comparable reference area whose past history is known or can be inferred. I selected the northern part of Flaherty Island as my reference area based on Edmonds' (1979) field study on range communities and the fact that reindeer have not been observed near Sanikiluaq since 1981 (S. Emikotailuk pers. comm.). Rather, hunters have consistently observed reindeer in the southwest and south-central regions of Flaherty Island since 1980-81.

During summer 1990 and 1991, I sampled vegetation communities near Sanikiluaq and from base camps on southwest and south-central Flaherty Island, and Tukarak Island (Figure 2-1). I determined locations of base camps according to current distribution of reindeer using information provided by hunters and previous ground and aerial surveys (Ferguson 1985, Arragutainaq *et al.* 1990). This ensured sampling of range communities along a grazing gradient, *i.e.,* from ungrazed (near Sanikiluaq) to grazed (southern Flaherty Island).

In the field, I used Edmonds' (1979) descriptions of range types and the following criteria (adapted from Fleck and Gunn 1982) to identify discrete range communities and select stands: a) the stand was representative of vegetation and landscape conditions in the general area; b) minimum size of sampled communities was 100 m x 50 m; c) areas disturbed by human activity were avoided, *i.e.,* all-terrain vehicle tracks; and d) the sampled area was recognizable on a 1:60,000 scale black and white aerial photo. At each stand I recorded the following environmental data: total number of pellet groups in a 200 m^2 belt transect, elevation (in 15 m (50 feet) intervals derived from a 1 : 50 000 scale topographical map), slope (s) class ($s < 1\%$, $1\% < s < 5\%$, and $s > 5\%$), substrate type (sand, gravel, organic, or rock), moisture class (xeric, mesic, hydric), and aspect (north, south, east, and west).

I sampled range communities using quadrats (n = 15 - 30) placed along a transect. Within the middle of a range community, I randomized the start of a transect by tossing a

stone over my shoulder. Direction of the transect was determined by tossing another stone. Occasionally this was repeated until the transect lay within the boundaries of the range community. Quadrats were spaced at 5 meter intervals on either the left or right hand side of the transect. I visually estimated percent cover of vegetation by projecting plants to the surface within a quadrat frame (50 cm x 50 cm) gridded into squares (5 x 5 cm) . Only one stratum was recognized and cover of bare ground and litter were estimated similarly. Sedges, mosses and crustose lichens were grouped into three general categories; other vascular plants and macrolichens were identified to species. Nomenclature follows Porsild and Cody (1980) for vascular plants, Hale (1979) and Vitt *et al.* (1988) for lichens. Voucher specimens were collected and deposited in the University of Alberta herbarium.

At eight stands, I also collected samples of standing crop by clipping all above-ground vegetation (macrolichens and vascular plants) within the lower half of the cover quadrat (25 cm x 50 cm). These samples were taken to the University of Alberta, where I sorted vascular plants (except sedges and grasses which were grouped by genus) and macrolichens to species. Lichens required thorough wetting in a tray of water prior to sorting and large samples were subsampled. I sorted shrubs to current and non-current growth and then oven-dried (24 h at 70° C) and weighed (0.001 g) all samples.

To compare aboveground biomass allocation of browsed and unbrowsed plants (Henry and Gunn 1991), I randomly collected 30 shoots each of *Salix glauca*, and *S. lanata* at stands that were used and unused by reindeer. Collections were made three times during the 1991 growing season. I sampled willows at used and unused stands within a 48 h period. Stands accessible to reindeer were located on south west Flaherty Island (Camps B, C, and D), and unused stands were located on northern Flaherty Island near Sanikiluaq (Figure 2-1). Stands were similar in species composition, moisture regime, substrate type, and topographic position. In the laboratory, shoots were sorted into current annual growth, live woody stems, flowers, and attached dead matter before oven-drying (70°C at 24 hours) and weighing (0.001 g).

Pooled samples were used to determine fiber and nutrient content in current growth of willows. From each collection of 30 shoots, I constructed three pooled samples based on current growth of 10 shoots. I ground current growth of each shoot in a Wiley mill through a No. 20-mesh screen. Fiber content was determined sequentially from neutral detergent fiber (NDF), acid detergent fiber (ADF), and H_2SO_4 lignin (Goering and Van Soest 1970, Mould and Robbins 1981) on pooled samples. Total cellulose was calculated as the sum of hemi-cellulose and cellulose. Nitrogen was determined using the Kjeldahl technique (A.A.O.C. 1984). Phosphorous was determined using the photometric method

(molybdovanadate reagent) on 2.0 g dry ashed samples (A.A.O.C. 1984). Potassium, magnesium, and calcium were determined by atomic-absorption flame spectrophotometry of the aliquot from 1.0 g dry ashed samples. I conducted all chemical analyses in duplicate.

Data analyses

I determined the relationship between percent cover and standing crop of vegetation using linear regression. Cover and biomass data were transformed using the arcsin and log transformation respectively to meet assumptions of the linear model (Zar 1984). A nested ANOVA was used to test differences in standing crop between ungrazed and heavily grazed areas; sites were nested within the two levels of grazing.

I classified stands based on mean cover of plant species using TWINSPAN, a polythetic divisive method of classification (Program 41: Cornell Ecology Package, Hill 1979). TWINSPAN is polythetic because it classifies stands on the basis of several species and divisive because sites are dichotomized into groups. Dichotomies are based on presence and abundance of differential (indicator) species, *i.e.* those species with clear ecological preferences. Indicator species are not restricted to a particular dichotomy. Characteristic species refer to species that are common but not restricted to a particular group of stands.

TWINSPAN delineated fourteen stands as representative of lichen-dominated range communities (community type A in Figure 2-2 and Table 2-2); I excluded one stand because it was atypical. With the remaining thirteen stands, I used a one-way ANOVA to test whether cover of lichens, and other plant growth forms were significantly different between heavily grazed, moderately grazed, and ungrazed lichen stands. Stands were classified according to number of pellet groups per $200m^2$ belt transect, *i.e.,* heavily grazed (number of pellet groups > 50), grazed (0 < number of pellet groups < 50), and ungrazed (no pellet groups). Residuals were inspected following ANOVA.

To assess the response of individual plant species to measured environmental variables, I conducted an ordination analysis on the thirteen stands classified as lichen-dominated range (community-type A in Figure 2-2) by incorporating both redundancy analysis (RDA) and principal components analysis (PCA) (see Jongman *et al.* 1987, ter Braak 1992). RDA is a direct gradient analysis based on a linear response of vegetation to measured environmental variables whereas PCA is an indirect gradient analysis. Thus, by incorporating both techniques, I partitioned observed variability of species composition in stands of lichen-dominated range into variation explained by measured environmental variables (RDA), and residual variation that was not explained by the

measured environmental variables (PCA). I used the CANOCO (version 3.10) software package (ter Braak 1992) to conduct this analysis. Cover data for plants, litter, and bare soil were log transformed (x + 1) to ensure that abundant and rare species were weighted more evenly (Jongman *et al.* 1987). Other transformations specific to linear ordination methods included centering by species and standardization by stands (Noy-Meir 1973, Noy-Meir *et al.* 1975, Noy-Meir and Whittacker 1977, Jongman *et al.* 1987).

Willow shoot data (biomass allocation, fiber and nutrient content) were analyzed with one-way ANOVAs to test for differences between browsed and unbrowsed samples. Regressions and ANOVAs were conducted using the Systat® software package (Wilkinson *et al.* 1992). All mean values are presented with associated standard errors (SE) unless otherwise specified.

Results

I established a total of eight base camps over two summers of field work (1990-91). Seven camps were located on Flaherty Island, and one camp was on Tukarak Island (Figure 2-1). Camps were accessed by boat and all stands sampled for cover (n = 35; 810 quadrats) and biomass (n = 8; 145 quadrats) were within hiking distance of camps. Ground cover of plants was significantly related to standing crop (Table 2-1).

Range communities on the Belcher Islands

TWINSPAN separated the 35 stands into five ecologically important community-types (Figure 2-2) and three species groups (Table 2-2). Associated indicator species and eigenvalues for each TWINSPAN division are in Figure 2-2. An overview of the physical and vegetative characteristics of each stand group follows. Edmonds' (1979) corresponding range descriptions are presented in brackets and are referred to in the remainder of the text. Figure 2-3 shows the typical spatial arrangement of these range communities with respect to drainage and moisture regime.

Community-type A (Mixed lichen-dwarf shrub flats)

This range community was characterized by relatively level, well drained sites. Lichens were the dominant growth form in this range type. The most abundant lichens were *Cetraria nivalis, C. islandica, Cladina mitis, C. rangiferina, Spharophous globosus,* and *Alectoria ochroleuca,* respectively. *Carex rupestris,* was the dominant monocot; *Festuca brachyphylla, Poa arctica* and *Luzula* spp. were present in most stands. Important forbs were *Epilobium latifolium, Pyrola grandiflora, Saxifraga tricuspidata, S. oppositifolia, Silene acaulis and Lathyrus japonicus.* The most abundant dwarf shrubs were *Vaccinium uliginosum, Dryas integrifolia, V. vitis-idaea,* and *Salix glauca.*

Community-type B (Barren bedrock ridges)

This range community was mostly unvegetated, and mean cover of bare ground was 72 ± 1%. Vegetation was restricted to small depressions, and cracks and crevices in the rock where soil could accumulate. These local depressions were dominated by mosses and sedges *(Carex* spp.). *Scirpus caespitosus* was also common in these hydric microsites. *C. nivalis, S. globosus, C. mitis, C. islandica, B. divergens, and A. ochroleuca* were found sporadically growing within the moss layer. *Umbilicaria* spp. *(U. hirsuta, U. proboscidia)* were important foliose lichens growing directly on rock. Dwarf shrubs

were limited in distribution and consisted mostly of *Empetrum nigrum, V. uliginosum,* and *D. integrifolia.*

Community-type C (Lichen-dwarf shrub gravel ridges)

This range community was characterized by raised gravel beaches. Bare ground was 43 ± 5% cover. Within these sorted gravel ridges, vegetation was limited to lichens *(Umbilicaria* spp., *A. ochroleuca, C. ericetorum, B. divergens,* and *S. globosus)* and sporadic distribution of *E. latifolium.* Between the gravel ridges, where soil conditions were more mesic, vegetation was similar to the mixed-lichen dwarf shrub flats in species composition and relative abundance.

Community-type D (Hummocky meadows)

These hummocky meadows were characterized by patterned ground due to frost action (Nicholson 1976). Bare ground represented 34 ± 4% of total cover. Frost boils were approximately 1 - 2 m in diameter whereas hummocks ranged in height from 0.2 - 1.0 m. Macrotopography (*i.e.* slope position and drainage) determined general moisture conditions and thus frost boils in stands with poor drainage had higher soil moisture and were softer than frost boils in better drained stands. Microtopography (relative size of hummocks) was an important physical characteristic that determined species distribution within these communities. Lichens were abundant on tops of hummocks, whereas sedges, dwarf shrubs, mosses and forbs were dominant on sides and bases of hummocks. Dominant shrubs included *V. uliginosum, D. integrifolia, Rhododendron lapponicum, Cassiope tetragona, S. lanata* and *S. arctica.* Forbs in this range type varied with moisture regime; in wetter sites, *Pedicularis* spp., *Bartsia alpina, Saxifraga aizoides, Equisetum scirpoides* and *Pinguicula vulgaris* were abundant, whereas in more mesic sites *Saxifraga tricuspidata,* and *S. oppositifolia* were present.

Community-type E (Sedge-moss stream beds)

This range community was generally hummocky, hydric-mesic in moisture regime, and typically located along stream banks. However, a stream was not a prerequisite of this range type as similar stands of vegetation were present along gently sloping seepage drainages and lake margins. Accordingly, lichens were scarce or absent in this community, although *Cetraria* spp. and *Cladina* spp. were still found in this community. Mosses and sedges *(Carex* spp.) dominated ground cover in this range community. *Salix arctica, V. uliginosum, S. reticulata, R. lapponicum, D. integrifolia, S. lanata,* and *Scirpus caespitosus,* were also abundant. Characteristic forbs were *Equisetum scirpoides, Polygonum viviparum,* and *P. grandiflora.*

Species group A Restricted xeric

This species group consisted of rare plants that represented less than 2% ground cover (except *Salix glauca)* and were found mostly in mixed lichen-dwarf shrub flats (well drained sites) (Table 2-2). The majority of species were forbs, with some lichens *(Dactylina arctica, Cladonia scabrialusca, C. deformis,* and *Stereocaulon alpinum)* and graminoids *(Poa arctica, Luzula spicata, L. nivalis,* and *Festuca brachyphylla).*

Species group B Widespread lichens and dwarf shrubs

Species group B consisted of the most widespread and diverse species. In general, abundance and distribution of species was related to general soil moisture characteristics. Abundance of lichens decreased from Stand group A to Stand group E whereas forbs and shrubs increased under wetter conditions (Table 2-2).

Species group C Restricted mesic

These species were most abundant under poorly drained conditions found typically in hummocky meadows and sedge-moss stream beds. Mosses, sedges *(Carex* spp.), *Salix arctica, S. lanata* and *S. caespitosus* were the most abundant species.

General overview of effects of reindeer on vegetation

Range communities in the south-west region of Flaherty Island were detrimentally affected by high densities of reindeer. The community affected most by reindeer was the "mixed lichen-dwarf shrub flats." Within heavily used areas, ground cover of broken unattached lichens, litter, and bared mineral and/or organic soil was greatest in this range type. Intact lichens were scarce. I also observed frequently used "game" trails and broken clumps of surface moss due to trampling. Vegetation growing in the mesic swales and dips between gravel ridges showed similar disturbance of lichens, and associated increases in cover of bared soil and litter.

In the hummocky meadows, I found patches of bared soil and exposed roots and rhizomes on the tops of hummocks. These exposed patches were restricted to the tops of large hummocks, *i.e.*, >30 cm in height. However, due to the abundance of gravel and bare soil (frost boils) inherent in those range communities, my sampling intensity was not high enough to detect differences between heavily grazed and ungrazed stands.

Intense browsing by reindeer had also decreased productivity and increased mortality of several stands of willows. Willows in areas of high reindeer densities had higher proportions of attached dead material compared to unbrowsed willows.

Reindeer and the "Mixed lichen-dwarf shrub flats" range type

Grazing intensity (as indicated by pellet-group densities) had a significant effect on cover of different plant categories. Abundance of lichens, and grasses and forbs decreased significantly as grazing intensity increased (Figure 2-4). Mosses showed a similar trend although differences were not significant. Conversely, cover of bare soil and litter was significantly greater at heavily grazed stands compared to moderately grazed and ungrazed stands (Figure 2-4). Dwarf shrubs also increased with grazing intensity but differences were not significant. Abundance of willows was not significantly different among stand groups.

I used RDA and PCA to partition observed variation in species composition of lichen-dominated range communities and to assess species-specific changes in abundance with respect to grazing intensity. I found that densities of pellet groups within a stand was the best variable for explaining observed variation among the 13 stands in the "mixed lichen dwarf shrub flats." In a redundancy analysis constrained by all measured environmental variables (elevation, slope and moisture class, aspect, substrate type, and pellet densities), the first axis accounted for 35% of observed variation (Table 2-3A). When the analysis was repeated but with pellet group densities as the only constraining variable, variation explained by the first axis declined to 30% (Table 2-3B). Thus, the other measured environmental variables added only 5% to the explanatory power of pellet group densities on the first axis.

Figure 2-5 shows the biplot and Table 2-3B shows the summary statistics of the ordination analysis of lichen communities. The first axis (RDA) was constrained to pellet group densities and thus represents a grazing gradient whereas the second axis (PCA) represents residual variation. Ungrazed stands are located on the left side of the origin and heavily grazed stands are located on the far right; grazed stands are intermediate and also located on the left side of the origin. The biplot shows clearly that as grazing intensity increases, abundance of lichens *(Cetraria islandica, C. nivalis, Cladina mitis, C. rangiferina, Bryocaulon divergens* and *Alectoria ochroleuca)* decreases whereas litter and bare soil increase. Most forbs were located close to the origin of the biplot and thus their response to grazing was difficult to determine. However, *Pyrola grandiflora, Epilobium latifolium, Saxifraga tricuspidata,* and *Lathyrus japponicus* were located on the left side of the origin suggesting a decrease due to intensive grazing; *P. grandiflora* and *S. tricuspidata* also show strong correlation with the second axis. Mosses (mostly *Racomitrium lanuginosum)* and sedges (mostly *Carex rupestris)* were more abundant in ungrazed and grazed stands, whereas dwarf shrubs *(i.e., Empetrum nigrum, and Dryas integrifolia)* were more abundant in heavily grazed stands.

Willows showed variable responses to grazing. *Salix reticulata* was more abundant at heavily grazed stands, whereas *S. glauca* showed no response to grazing intensity and together with *V. uliginosum* was strongly correlated to the second axis. *Rhododendron lapponicum* and *V. vitis-idaea* also showed strong correlation with the second axis.

Similarity in composition and abundance of species between stands (beta diversity) is a function of distance between stand locations within a biplot (ter Braak 1983). From the ordination biplot (Figure 2-5), I identified three main groups of related stands. The first group consisted of 2 ungrazed stands located in the top left quadrant of the biplot. These stands were characterized by high cover of lichens (*C. islandica, C. nivalis*, and *C. cucullata)* willow *(Salix glauca)* and forbs *(Saxifraga tricuspidata, Pyrola grandiflora, and Lathyrus japponicus).* The second group, located in the bottom-left quadrant, consisted of two ungrazed and 4 grazed stands. These stands had similar cover of *Cetraria* spp., and had higher cover of mosses and sedges. *Epilobium latifolium* was the dominant forb, and *R. lapponicum, V. uliginosum,* and *V. vitis-idaea* were important shrubs. *Salix glauca* was not abundant at these stands. The final group consisted of five heavily grazed stands located to the right of the origin. Ground cover at these heavily grazed stands was dominated by litter (dead vascular tissue and dead and broken lichen thalli) and bare soil. *Salix reticulata* and the dwarf shrubs *E. nigrum* and *D. integrifolia* were more abundant at these heavily grazed stands.

Standing crop of vegetation

Mixed lichen dwarf shrub sedge moss flats

Standing crop of lichens was significantly less in heavily grazed areas (16.3 $\pm$ 26.8 g/m^2) compared to ungrazed areas (216 $\pm$ 19.2 g/m^2) (ANOVA, $F = 36.78$, df = 1, $p < 0.0001$). Mean standing crop of ungrazed lichen stands ranged from 174 to 273 g/m^2 whereas heavily grazed stands had standing crop of lichens that were 12 to 20 g/m^2 (Table 2-4). *Cetraria nivalis, C. islandica, Cladina mitis,* and *C. rangiferina* were the most abundant lichens in sampled stands (Table 2-4). Dwarf shrubs and forbs were the second and third most abundant component of standing crop at these stands (Table 2-4). Standing crop between sites within grazing 'treatments' (ungrazed vs. heavily grazed) was not significantly different (ANOVA, $F = 3.1$, df = 3, $p = 0.14$).

Lichen-dwarf shrub gravel ridges and Sedge moss stream beds

Standing crop of vegetation at one stand in the gravel ridge range type, and two stands in sedge moss stream beds are presented in Table 2-4. Lichens and dwarf shrubs *(Dryas integrifolia)* were the dominant plant types in the gravel ridge range type. Dwarf

shrubs, willows, and lichens were the most abundant plants in the two stands sampled in sedge moss stream beds.

Willow shoots

Biomass allocation

Twigs of *Salix glauca* collected in stands of high reindeer densities had significantly lower proportions of current growth and significantly higher proportions of attached dead material compared to twigs collected at associated unused stands (Table 2-5). A proportional decrease in current growth and increase in dead material was similar for twigs of *S. lanata* collected at the same sites (Table 2-5). *Salix glauca* sampled from the moderately used stand had a significantly higher proportion of live stems compared to the unused stand. *Salix lanata* at the moderately used stand had a greater proportion of current growth and a smaller proportion of live stems compared to the unused stand.

Fiber and nutrient composition

There were no detectable trends in either total cellulose or lignin content of current growth in *Salix glauca* or *S. lanata* between heavily used and unused stands. However, current growth in both species consistently had higher levels of nitrogen and phosphorous at heavily used stands compared to twigs sampled at unused stands; calcium content also showed a similar trend (Tables 2-6 and 2-7).

Cellulose and lignin were significantly higher in current growth of *S. glauca* sampled from a moderately used stand compared to an unused stand (Table 2-6). *Salix lanata* also exhibited this trend (Table 2-7). With respect to nutrients, *S. glauca* had a higher concentration of calcium whereas *S. lanata* had higher potassium content at the moderately used stand. Concentration of magnesium was significantly higher in current growth of *S. lanata* from the unused stand compared to the moderately used stand.

Discussion

Classification of range communities

Edmonds' (1979) classification of range communities on the Belcher Islands was reliable and relatively easy to implement in the field. Edmonds recognized seven distinct range communities. I present a description of five range communities. I sampled primarily lichen range communities and did not sample "sand dune" areas as Edmonds (1979) did because those range communities were quite restricted in their distribution and abundance.

Based on my field data, I was not able to consistently separate Edmonds' (1979) "mixed lichen-dwarf shrub-sedge moss hummocky meadows" and "dwarf shrub-sedge-moss hummocky meadows" with TWINSPAN. Rather, stands were combined under one range type as "hummocky meadows;" the difference between the two range types remained subjective. TWINSPAN was unable to identify appropriate indicator species and thus consistently distinguish between Edmond's (1979) two hummocky range types because of similarity in species composition, inherent heterogeneity of these communities, and inadequate sampling intensity within a stand. The same suite of species was present in both range types and patterns of abundance and distribution of plants were due to differences in moisture regime and microtopography. As a result of the patchy distribution of plants and high cover of bare ground, *i.e.,* frost boils accounted for approximately 35% of total ground cover, there was much variability associated with estimates of mean cover of plant species. Also, regular spacing of quadrats at 5 m intervals along a transect may have been inappropriate for this patterned ground habitat. Perhaps a more suitable sampling protocol in patterned ground range communities would have been to randomize positions along the transect. Nevertheless, Edmonds' (1979) distinction between these range communities is ecologically important and should be realized for an assessment of habitat use by reindeer (Chapter 3).

Range communities on the Belcher Islands are characteristic of southern arctic tundra (see Bliss *et al.* 1981, Ahti and Oksanen 1990). Lichen dominated range communities, *i.e.,* "mixed lichen-dwarf shrub flats," on the Belchers are dominated by *Cetraria* species rather than *Cladina* species. Edmonds' (1979) estimate of standing crop of lichens at one stand (267 g/m^2) was similar to my estimates of standing crop of lichens at three ungrazed lichen stands (174, 201, and 273 g/m^2 respectively). Adjacent to the Belchers in northwest Quebec, standing crop of lichens within the 400-499 and 500-599 mm precipitation zones is approximately 256 and 122 g/m^2 respectively

(Crete *et al.* 1990). In contrast to the Belchers, *Cladina* and *Cladonia* species were more abundant than *Cetraria* species in that region of forest tundra.

Lichen range communities on Southampton Island and Coats Island are similar to the Belchers in that *Cetraria* species are also more abundant than *Cladina* species on those islands (Parker 1975, Adamczewski *et al.* 1988, Ouellet 1992). Standing crop of lichens on the Belchers is greater than mean lichen biomass of important lichen range on Southampton Island (80-100 g/m^2; Parker 1975), (126 g/m^2; calculated from Ouellet 1992) and substantially greater than Coats Island (27-30 g/m^2) (Adamczewski *et al.* 1988). However, compared to lichen range in Sweden, Alaska, and Russia, lichen range on the Belcher Islands (like Southampton Island, Parker 1975) is low in lichen production (Edmonds 1979).

Estimates of standing crop in "lichen-dwarf shrub gravel ridges" was representative of that range type, but estimates of standing crop in "sedge-moss stream beds" was low. The sedge-moss stream beds range type is likely the most productive range community with respect to standing crop of vascular species. Thus, the two sites sampled should be considered at the low end of the scale of standing crop for this range type. Site 2-1 was a mesic stand located along a seepage drainage and had a high abundance of lichens. Site 2-2 was hummocky and lichens were present on the tops of hummocks. Water accounted for approximately 10% of ground cover. Further sampling is required in sedge moss stream beds and along lake margins to accurately estimate standing crop of vascular plants.

Overgrazing and lichen range

In the absence of vegetation data prior to the introduction of reindeer in areas now occupied by these animals, a fundamental assumption of this study is that plant species which are now absent or rare in areas used by reindeer were similar in abundance to corresponding communities in unused areas. In areas used heavily by reindeer, ungrazed "reserves" of lichens and vascular plants located between boulders and otherwise inaccessible to reindeer provide circumstantial evidence that supports this assumption.

My principal conclusion is that introduced reindeer on the Belcher Islands have caused a significant decline in abundance of lichens in the south west arm of Flaherty Island; reindeer have overgrazed lichen-dominated range communities in this region. I consider "overgrazing" as a change in forage cover (biomass) of a plant community arising from the combined effects of grazing, browsing, and trampling that is deleterious to future forage and animal production (see Wilson and Macleod 1991). Overgrazing results in the nearly complete removal or disturbance of aboveground vegetation. In

lichen range communities, overgrazing by reindeer involves the near complete removal and disturbance of the lichen-moss layer. Lichens and clumps of moss are dislodged. Lichen thalli are fragmented to small pieces < 2 cm, and underlying organic or mineral soil is exposed.

A sequence of overgrazing of lichens was evident both in terms of geographical area and range type. Severity of overgrazing decreased as one traveled north from the southern region of the south west arm of Flaherty Island towards Sanikiluaq, *i.e.,* a grazing gradient. Reindeer on the Belcher Islands show strong fidelity to the south west region of Flaherty Island (Chapter 3). Moderately grazed lichen stands at camps A and C were relatively similar in cover of lichens and other plant components (Figure 2-4 and 2-5) compared to ungrazed stands at camps 3 and S (Figure 2-1). With respect to range, the "mixed lichen-dwarf shrub flats" range type was the most susceptible and evidence clearly showed the severity of overgrazing. Based on field observations, I subjectively rank the "lichen-dwarf shrub gravel ridges" and the "mixed lichen-dwarf shrub-sedge-moss hummocky meadows" as the second and third most sensitive range communities to overgrazing by reindeer. Overgrazing in the hummocky meadow range type was restricted to removal of vegetation from the tops of large hummocks. Presumably, this disturbance occurs in winter when reindeer are foraging for lichens. Kongsrude (1988) observed similar effects of caribou on the raised rims of polygonal peat plateaus south of Churchill, Manitoba. She estimated that 14% of vegetation on raised rims was removed and concluded that winter foraging by caribou was an intense form of disturbance; in addition to actual removal of lichens, below ground biomass of disturbed vascular plants was destroyed.

The pattern of overgrazed lichen range on the Belchers is similar to patterns reported for degradation of preferred range by Himalayan thar *(Hemitragus jemlahicus)* introduced to New Zealand (Caughley 1970) and introduced reindeer on St. Matthew (Klein 1968) and South Georgia Islands (Leader-Williams 1988). In a test of Riney's (1964) model of irruptive oscillations in ungulates, Caughley (1970) sampled thar from areas at different distances from the initial point of liberation. He found an increase in juvenile mortality and an associated decrease in food supply (cover of tussock grasses) along a transect from the dispersal front to the range center. The pattern of overgrazing by reindeer in the south west region of Flaherty Island is functionally similar to Caughley's (1970) observations on forage depletion but different with respect to scale. Overgrazing in this region is likely a result of the activity of a large aggregation of reindeer (at least 200-250 animals) that occupies this

area. As the "core" area becomes overgrazed in south west Flaherty Island, reindeer travel greater distances to forage.

The progression of overgrazing of lichens and willows on the Belchers is similar to overgrazing by reindeer on St. Matthew Island and South Georgia Island where available range was restricted and dispersal was more limited. Klein (1968) observed effects of heavy reindeer use on winter range on St. Matthew Island as early as 1957 - 13 years after the introduction of reindeer. Lichens had been seriously depleted through the combination of winter grazing, trampling, and shattering, and removal of dry shattered pieces of lichens by the strong winds (Klein 1968). By 1963, Klein (1968) noted that willows had begun to show signs of deterioration as a result of heavy winter browsing. In sum, he concluded that summer range seldom suffers from over utilization and that winter range condition varied with use and population density and was therefore the most important factor in population control. My results show that 12-13 years after their introduction, reindeer on the Belchers have also over utilized areas of lichen range. Furthermore, willows show signs of deterioration due mostly to heavy browsing in spring and summer (see discussion below).

In a similar situation on South Georgia, reindeer first depleted lichens in dry meadow and fellfield communities upon introduction or immigration to new areas. Preferred vascular species *(Deschampsia antarctica* and *Acaena magellanica)* in dwarf shrub sward and mesic communities were overgrazed in summer (Lindsay 1973, Kightley and Smith 1976). When reindeer reached peak densities, tussock grasslands were affected severely in winter. The sequence of overgrazing in tussock grassland was related to the duration of time that an area had been occupied (Leader-Williams 1988). More recently, Ouellet (1992) found that caribou reintroduced to Southampton Island are increasing rapidly and have also negatively affected areas of lichen range. Thus, degradation of the "mixed lichen-dwarf shrub flats" on the Belchers further substantiates the observation that lichen range is the first habitat type to be detrimentally affected by non-migratory reindeer introduced to Arctic and subantarctic environments (Klein 1968, Lindsay 1973, Leader-Williams 1988, Swanson and Barker 1992).

It is difficult to quantitatively differentiate between direct effects of grazing and tramping by wild *Rangifer* in the field. However, Pegau (1970a) estimated the effects of trampling by reindeer on their summer range near Nome, Alaska, and found that after one season on a large *Eriophorum - Carex* - dwarf shrub meadow, trampling dislodged 68% of the lichens and 16% were broken into fragments less than 1.25 cm in length. Gaare and Skogland (1975) estimated that wastage of lichens was ten times as great as

the actual biomass consumed by reindeer in winter. Similarly, mean decline in biomass of lichens and vascular plants on summer range in Alaska was six to ten times greater than biomass consumed by reindeer (White and Trudell 1980). Thus the net effect of reindeer and caribou on range is a result of both grazing and trampling. My results show that lichen range in south west Flaherty Island has been severely "overgrazed" by reindeer. The effects of grazing and trampling are reflected by reduced cover of lichens, grasses, and forbs, and an increase in litter (including dead and unattached lichen fragments) and bare ground. Grazing and trampling of lichen range occurs throughout the entire year with the trampling effect most important in summer when lichens are dry and less palatable (Pegau 1970a). A decrease in abundance of graminoids in overgrazed lichen range on the Belchers was different than overgrazed range on St. Matthew Island. Klein (1968) found that cover of sedges and grasses increased under continued and increasing grazing pressure. Low abundance of graminoids in overgrazed range on the Belchers is likely a result of heavy trampling. Once bare ground is exposed by high reindeer densities, continual trampling of the range may destroy the meristematic tissue of graminoids (see Archer and Tieszen 1980) and impede establishment of new growth. In this way, overgrazing exposes bare soil and trampling maintains it.

In contrast to a decrease in lichens, grasses, and forbs, the evergreen dwarf shrubs *Dryas integrifolia,* and *Empetrum nigrum,* were more abundant at heavily used stands. These findings are comparative to *Calluna - Cladina* heaths in northwestern Finnish Lapland. Regular grazing by reindeer in early winter decreased abundance of lichens whereas dwarf shrubs (families Ericaceae and Empetraceae) increased (Helle and Aspi 1983). Three hypotheses that may explain these observations are that dwarf shrubs are: 1) unpalatable and not eaten by reindeer (Henry and Gunn 1991); 2) more resistant to the effects of grazing and trampling; or 3) less competitive than reindeer lichens which have reached the climax stage (Helle and Aspi 1983).

The salient question regarding overgrazed lichen range on the Belchers is: how long will it take for overgrazed lichen range to recover and will it ever regain former productivity? Studies by Palmer and Rouse (1945) and Pegau (1970b) in Alaska, Skunke (1969) in Sweden, and Chernov (1985) in Russia, suggest that lichen range may require 30 - 50 years following heavy grazing to recover to former levels of biomass. They emphasized that time required for recovery of lichens was dependent on climatic conditions, amount of tissue remaining after overgrazing, and the influence of vascular plants. More recently, Klein (1987) sampled lichen range that was overgrazed by reindeer on St. Matthew Island (Klein 1968) and found that even after 22

years, biomass of lichens was less than 10% of its former abundance and that the species of lichen that were most abundant were not preferred species. These findings are important given the relatively high rate of growth of lichens in Alaska (Pegau 1968). In a related study on succession of lichens in forest tundra following fire, Scotter (1964) outlined three stages of succession with respect to dominant lichens. He found that important forage lichens such as *Cladina mitis* and *Cladonia amaurocraea* reached their greatest development in the second stage, 11 to 50 years post fire, whereas the "reindeer lichens" *Cladina rangiferina* and *C. stellaris* reached their former abundance in the third stage, 90 to 120 years after fire. Although, tundra range on the Belcher Islands is not identical to forest tundra in northern Saskatchewan, Scotter's (1964) study shows how disturbance, *i.e.*, fire, resets succession in a plant community and that composition and abundance of lichens through time are dependent on climate, soil conditions, growth rates of lichens, and competing vascular and nonvascular plants. Thus, it is likely that overgrazed areas on the Belchers will require a minimum of 20 - 50 years in the absence of continued use by reindeer to recover. However, with continued use (trampling) by reindeer, recovery and species composition may be altered indefinitely and lichen production may never recover in overgrazed areas.

Evidence of range use from pellet transects and observations by hunters suggest that reindeer use the southwest and south-central regions of Flaherty Island, Inetalling Island, Mukpollo Peninsula intensively, whereas Kugong Island, Tukarak Island, and central and northern Flaherty Island have not been occupied by reindeer for extended periods of time (Chapter 3). Although I was not able to sample lichen range extensively throughout the four main islands, I believe that a majority of lichen range on the Belcher Islands is either moderately grazed or unused by reindeer at the present time. Edmonds (1970) indicated that the most productive lichen range on the Belchers was on Tukarak Island, Kugong Island, and central Flaherty Island; her range map indicated that there was little prime lichen range in the southwest and south-central region of Flaherty Island. However, this is the region where hunters see the most reindeer (L. Arragutainaq pers. comm.). I think that Edmonds' (1979) range map was essentially accurate although she underestimated the abundance of lichen range in the southwest region of Flaherty Island. Lichen range is present but it occurs in relatively small areas which may not have been recognizable from Landsat imagery. Lichen range on Tukarak Island is extensive and productive (Table 2-4) and has not been used by reindeer.

Willows

Due to logistic constraints, samples of willows were paired between areas with and without reindeer at three periods during the growing season. These paired samples were

not replicated and therefore it was not possible to estimate an error term associated with the "browsing" treatment (Hurlbert 1985, Webster 1992). Nevertheless, observed differences in biomass allocation and nutrient concentration in willows between browsed and unbrowsed stands are important in light of two reasons. Firstly, stands were selected based on similar environmental characteristics (topography, moisture regime, and species composition) and as representative of willows in the general area. Secondly, willows (*Salix* spp.) are generally known for their extensive root systems which act as storage organs for carbon and nutrients (Chapin 1980a, Chapin *et al.* 1980, Chapin *et al.* 1986, Chapin and Shaver 1985), their rapid rates of growth and reproduction through coppice suckering (DeGrosbois *et al.* 1991), and their ability to recover from brief episodes of intense browsing (Henry and Gunn 1991).

Response of willows to defoliation is dependent on timing, frequency, and intensity of tissue removal (Archer and Tiezen 1980, Chapin 1980a and 1980b, Chapin *et al.* 1980, Ouellet 1992). Willows are most susceptible to browsing early in the growing season because a high proportion of carbohydrates and total nutrient stores (N and P) are in the leaves (Chapin *et al.* 1980). Archer and Tiezen (1980) found that defoliated *S. pulchra* produced significantly less current growth compared to controls in the following year and that twigs defoliated later in the growing season produced more biomass than twigs defoliated early in the season. Ouellet (1992) showed that *S. lanata* had a similar response; when twigs were clipped in late summer production of leaves the following year was unaffected whereas individuals clipped early in the growing season had lower leaf production. In addition, continual and intense (*i.e.*, a large proportion of available tissue) removal of tissue may have a strong effect on plant fitness because it invokes a net loss in nutrients and carbohydrate (Chapin *et al.* 1980). Given the large underground stores of carbon and nutrients, chronic, severe defoliation must be maintained over successive years for mortality of even part of the shrub (roots) to occur (see Chapin 1980a). Thus, given the high proportion of attached dead material and low proportion of current growth in twigs of *S. glauca* and *S. lanata* in heavily used stands compared to unused stands, I reason that reindeer begin browsing in spring (post-calving) and that browsing removes a large proportion of photosynthetic tissue. The willows were not able to compensate (sensu McNaughton 1983) for tissue lost to browsing as the willows on Rideout Island did following a brief episode of heavy browsing by caribou (Henry and Gunn 1991). Browsing pressure in south west Flaherty Island is likely sustained throughout the growing season and willows at these heavily used stands have probably been browsed repeatedly year after year.

Differences in aboveground biomass allocation in willows at the moderately used and unused stand seem to indicate that at lower browsing pressure, *S. glauca* and *S. lanata* were able to compensate for tissue lost to browsing. *Salix glauca* had similar percent biomass of current growth and a larger proportion of live twigs whereas *S. lanata* had proportionally greater current growth and less live twigs at the moderately used stand. Assuming that compensatory growth was the main reason for observed differences in biomass allocation to current growth and live twigs between stands, I speculate that either reindeer prefer *S. glauca* over *S. lanata* and thus browse *S. glauca* more intensively, or that *S. lanata* has a stronger compensatory response to browsing than *S. glauca*.

Differences in nutrient levels in current growth of willows are more difficult to relate directly to browsing because of potential differences in soil conditions between stands. Site specific differences in soil nutrients can cause differences in nutrient content of willow tissue (Chapin 1980b, Ericsson 1981, Simon *et al.* 1990). However, concomitant with elevated soil nutrient levels, specifically nitrogen and phosphorous, one would expect higher production (biomass) of leaves and current stems (Shaver and Chapin 1980, Ericsson 1981, Chapin and Shaver 1985, Simon *et al.* 1990). However, this was clearly not the case for willows sampled at heavily used compared to unused sites. I observed a significantly lower proportion of current growth and a greater concentration of nitrogen and phosphorous, and calcium to a lesser extent, in willows at heavily used stands. My results more closely follow Ouellet's (1992) experiments where he showed that simulated browsing of *Salix lanata* resulted in increased nitrogen and phosphorous content in leaves during the year of treatment. Concentration of Ca also increased in leaves when *S. lanata* was clipped in early and late summer (Ouellet 1992). Thus, I argue that potential differences in soil nutrient levels between sites does not fully explain the observed patterns of nutrient concentration and biomass allocation in current growth of willows from heavily used stands. Rather, I interpret the increased levels of nitrogen and phosphorous as a compensatory response of willows to browsing.

Cellulose and lignin content were greater in current growth of twigs from moderately used stands compared to unused stands. This suggests that regrowth following moderate browsing has greater abundance of plant cell wall material and lignified tissue. The most probable explanation is that stems are produced in greater abundance over leaves. On Rideout Island where caribou overgrazed vegetation in a single growing season, *Betula glandulosa* had significantly greater proportion of live twigs and less leaves than shrubs on a nearby mainland site the following year (Henry and Gunn 1991). Similarly, DeGrosbois *et al.* (1991) found that following complete canopy removal of *Salix*

arbusculoides, regrowth of aboveground biomass was primarily through stem growth rather than leaf production.

Willows are important forage to Belcher Island reindeer; in summer willows account for greater than 97% of the diet (Chapter 3). I tentatively conclude that frequent and sustained browsing by reindeer in summer has affected biomass allocation and nutrient concentration of current growth in willows. Intense browsing has decreased productivity but elevated levels of nitrogen and phosphorous in current growth of willows. The net result has been an increase in proportion of attached dead material, *i.e.* mortality of willow twigs, in areas used heavily by reindeer. These results are comparable to habitat relationships of West Greenland caribou. Thing (1984) described a caribou induced successional relationship between stands of *Salix glauca* and *Betula nana*, and *Poa pratensis*. He suggested that healthy stands of willow and birch were supported by low densities of caribou. "With increasing caribou numbers, browsing pressure was intensified during leaf emergence in post-calving and summer dispersal. This browsing consisted of stripping the branches of the leaves and removal of terminal buds. The effect of intense browsing for several consecutive summers eventually meant destruction of the shrubs and its subsequent disappearance" (Thing 1984. p 35-36). As a result of shrub removal and input of nutrients via feces and urine, lush growth of grasses *(P. pratensis)* was favored and maintained by intensive cropping. These grazing lawns were maintained until the caribou population decreased and succession moved towards heterogeneous stands of grasses, forbs, and shrubs (Thing 1984).

Although lichens have been typically used as an indicator of range quality and quantity for *Rangifer* (Palmer and Rouse 1945, Klein 1987, Skogland 1990, Swanson and Barker 1991), Crete *et al.* (1990) suggest that abundance of deciduous shrubs in summer are an important regulating factor in the dynamics of George River caribou. Consequently, use of willows by reindeer on the Belcher Islands should be monitored more extensively to test the hypothesis that severe browsing in summer causes mortality of twigs and roots. If willows continue to be the major summer forage, fall body condition of reindeer may be negatively affected.

In conclusion, patterns of range use by introduced reindeer on the Belcher Islands has resulted in severe overgrazing of lichen dominated range communities in the southwest region of Flaherty Island. Reindeer have also increased mortality of willows, species generally known for their ability to tolerate browsing. These results show that heavily used range on the Belcher Islands has been overgrazed despite the continuing growth of the reindeer population.

Table 2-1. Relationship between ground cover (per cent) and aboveground standing crop (g/m^2) of different plant growth forms.

Plant growth form	Regression equation	R^2	p	n
Macro-lichens	log (y + 1) = 0.05 + 0.51x*	0.79	0.0001	145
Willows (current growth)	log (y + 1) = 0.05 + 0.01x	0.87	0.0001	143
Dwarf shrubs (current growth)	log (y + 1) = 0.04 + 0.18x	0.78	0.0001	145
Graminoids and forbs	log (y + 1) = 0.03 + 0.16x	0.66	0.0001	145

* Where y = biomass (g/m^2); and x = arcsin (% cover)

Table 2-2. Cover values for vegetation within five community-types as delimited by TWINSPAN (see Figure 2-2). Species and stands are arranged in an ordered two-way table (Hill 1979).

	STAND GROUPS				
Community-type	A	B	C	D	E
Number of Stands	(14)	(3)	(7)	(12)	(2)
Edmonds' (1979) Range Classification	Mixed lichen-dwarf shrub flats	Barren bedrock ridges	Lichen-dwarf shrub gravel ridges	Hummocky meadows	Sedge-moss stream beds
SPECIES GROUP A					
Salix phlebophylla	+	-	-	-	-
Salix herbacea	1	-	-	+	-
Petasites frigidus	+	-	-	-	-
Dactylina arctica	+	-	-	-	-
Cladonia scabrialusca	+	+	+	+	+
Cladonia deformis	+	-	+	-	-
Taraxacum lacerum	+	-	-	-	-
Ranunculus pedatifidus	+	-	-	-	-
Papaver radicatum	+	-	-	-	-
Lathyrus japonicus	1	-	-	-	-
Draba spp.	1	+	+	+	+
Elymus arenarius	+	-	-	-	-
Potentilla nivea	+	+	-	-	-
Melandrium apetalum	+	-	-	-	-
Cerastium alpinum	+	-	-	-	-
Astragalus eucosmus	+	-	-	+	-
Armeria maritima	+	-	-	+	-
Festuca brachyphylla	+	+	+	+	-
Salix glauca	2	1	1	1	-
Stereocaulon alpinum	+	-	+	+	-
Poa arctica	1	+	+	+	+
Luzula spp.	1	+	+	+	+
Pertusaria dactylina	+	+	+	+	-
Sheperdia canadensis	1	-	+	-	-
Saxifraga tricuspidata	1	+	1	-	-
SPECIES GROUP B					
Loiseleuria procumbens	+	-	1	-	-
Cladonia squamosa	+	-	+	-	-
Cladonia cornuta	+	-	+	+	-
Vaccinium vitis-idaea	2	+	1	1	1
Pyrola grandiflora	1	1	1	+	1
Thamnolia vermicularis	1	+	+	+	+
Sphaerophus globosus	1	1	1	1	1
Cladina mitis	1	1	1	1	+
Cetraria nivalis	3	1	2	2	2

Table 2-2. Continued

Cetraria islandica	2	1	1	1	1
Stellaria longipes	+	-	+	+	-
Empetrum nigrum	1	1	1	1	+
Cladina rangiferina	1	1	1	1	1
Vaccinium uliginosum	3	1	2	3	3
Salix reticulata	1	+	1	1	3
Rhododendron lapponicum	1	+	1	2	2
Arctostaphylos rubra	1	+	1	1	1
Polygonum viviparum	1	+	1	1	1
Mosses	3	1	2	2	4
Dryas integrifolia	3	1	3	3	2
Silene acaulis	1	1	1	1	+
Saxifraga oppositifolia	1	+	+	+	-
Cladonia spp.	+	+	+	+	+
Cladina stellaris	1	1	+	1	1
Cladonia amourocrea	1	-	+	+	-
Cetraria cucullata	1	+	1	1	+
Bryocaulon divergens	1	1	1	1	1
Alectoria ochroleuca	1	1	1	1	+
Alectoria nigricans	1	+	1	+	+
Umbilicaria spp.	+	2	1	+	-
Cladonia pyxidata	+	+	+	+	+
Epilobium latifolium	1	+	1	+	-
Cetraria ericetorum	1	1	1	+	1
SPECIES GROUP C					
Pedicularis spp.	+	-	+	+	+
Carex spp.	2	2	2	3	4
Tofieldia pusilla	+	+	+	+	+
Bartsia alpina	+	+	+	1	+
Salix arctica	1	1	1	1	3
Pinguicula vulgaris	+	-	+	+	-
Juncus spp.	-	+	+	+	+
Lycopodium selago	-	+	-	+	-
Cassiope tetragona	-	-	-	1	-
Saxifraga aizoides	+	-	+	1	-
Rubus chamaemorus	-	-	+	-	+
Equisetum scirpoides	-	-	+	+	+
Salix lanata	+	-	1	1	1
Diapensia lapponica	-	+	+	-	-
Saxifraga aizoon	-	-	+	-	-
Scirpus caespitosus	+	1	+	+	1

Numbers indicate mean cover values on a scale of 1 to 5 using the following categories based on ground cover: 1, 0.01-1.9%; 2, 2-4.9%; 3, 5-9.9%; 4, 10-19.9%, 5, 20-100%; +, <0.01; -, absent. *Luzula* spp. consist of *Luzula nivalis*, and *Luzula confusa*. *Umbilicaria* spp. consist of *U. hirsuta*, and *U. proboscidia*. *Pedicularis* spp. consist of *P. flammea*, and *P. hirsuta*, *Juncus* spp. consist of *J. albescens*, *J. biglumis*, and *J. castenaus*.

Table 2-3. Summary of ordination analyses for lichen-dominated range communities on the Belcher Islands. The first axis is constrained to measured environmental variables (redundancy analysis), whereas the second, third, and fourth axes are unconstrained (principal components analysis).

A) First axis constrained to all measured environmental variables.

	Axes			
	1	2	3	4
Eigenvalues	0.350	0.253	0.137	0.075
Species-environment correlations	0.997	0	0	0
Cumulative percentage variance				
of species data	35.0	60.3	74.0	81.5
of species-environment relation	50.1	0	0	0

B) First axis constrained to pellet-group densities only (*via* forward selection of environmental variables).

	Axes			
	1	2	3	4
Eigenvalues	0.299	0.253	0.151	0.094
Species-environment correlations	0.934	0	0	0
Cumulative percentage variance				
of species data	29.9	55.2	70.3	79.7
of species-environment relation	100	0	0	0

Table 2-4. Mean (± SE) standing crop of vegetation (g/m^2) at eight stands sampled on the Belcher Islands.

PLANT SPECIES	STAND NUMBER† 1-2	B-3	3-2	3-3
Range Type	Mixed lichen dwarf shrub flats	Mixed lichen dwarf shrub flats	Mixed lichen dwarf shrub flats	Mixed lichen dwarf shrub flats
Number of pellet-groups / $200m^2$	90	116	0	0
Fruticose lichens				
Alectoria ochroleuca	3.28 (0.79)	0.34 (0.07)	9.52 (2.25)	7.54 (2.23)
Bryocaulon divergens	3.43 (0.83)	0.92 (0.28)	8.31 (2.18)	17.86 (3.06)
Cetraria islandica	0.51 (0.14)	0.85 (0.28)	25.55 (6.11)	24.76 (3.78)
Cetraria nivalis	4.97(1.20)	3.38 (0.46)	39.64 (6.70)	90.85 (9.35)
Cladina mitis	0.24 (0.10)	1.96 (0.65)	4.81 (1.39)	20.34 (5.56)
Cladina rangiferina	1.67 (0.82)	0.50 (0.12)	65.56 (48.74)	61.49 (18.12)
Cladonia amourocrea	-	0.02 (0.02)	5.27 (1.66)	8.67 (5.39)
Sphaerophous globosus	3.79 (1.01)	2.98 (0.73)	7.36 (2.24)	14.54 (5.07)
Others	2.82 (0.64)	1.04 (0.31)	8.22 (1.62)	27.99 (4.78)
Total	20.70 (3.84)	11.98 (1.83)	174.24 (53.17)	273.97 (30.25)
Forbs				
Polygonum viviparum	-	0.05 (0.03)	0.15 (0.05)	0.25 (0.09)
Pyrola grandiflora	-	2.47 (0.82)	3.05 (1.34)	0.36 (0.30)
Saxifraga oppositifolia	-	-	0.01 (0.01)	-
S. tricuspidata	-	-	-	-
Others	0.24 (0.22)	0.09 (0.06)	3.21 (1.12)	1.74 (1.03)
Total	0.24 (0.22)	2.62 (0.83)	6.41 (1.75)	2.35 (1.12)
Dwarf Shrubs (current growth)				
Dryas integrifolia	12.55 (5.12)	60.27 (23.76)	53.65 (10.42)	3.08 (1.23)
Empetrum nigrum	5.66 (4.09)	9.69 (4.26)	13.73 (7.85)	20.94 (6.66)
Rhododendron lapponicum	1.27 (1.27)	-	8.34 (5.31)	6.76 (3.12)
Vaccinium uliginosum	6.63 (1.91)	11.51 (3.09)	6.83 (1.91)	7.61 (2.12)
Vaccinium vitis-idaee	4.78 (1.40)	9.61 (2.71)	0.87 (0.32)	19.86 (2.90)
Others	-	-	1.33 (0.98)	1.74 (0.92)
Total	30.89 (6.94)	91.08 (20.81)	83.41 (12.24)	59.97 (7.41)
(twigs)				
D. integrifolia	41.62 (21.30)	37.47 (11.71)	132.82 (29.74)	5.81 (2.51)
E. nigrum	4.28 (2.14)	3.96 (1.67)	12.45 (8.16)	12.81 (4.07)
R. lapponicum	2.34 (2.34)	-	9.35 (5.47)	13.87 (7.23)
V.uliginossum	17.87 (6.89)	12.23 (3.47)	34.49 (9.78)	29.63 (8.33)
V. vitis-idaee	3.53 (1.36)	1.86 (0.56)	-	16.69 (6.37)
Others	-	-	1.11 (1.05)	0.94 (0.64)
Total	69.65 (21.87)	52.40 (11.81)	189.10 (53.15)	79.52 (11.14)
Willows (current growth)				
Salix arctica	-	-	-	1.52 (0.99)
S. glauca	1.15 (0.64)	0.35 (0.20)	-	-
S. reticulata	0.02 (0.02)	0.51 (0.50)	0.43 (0.41)	0.15 (0.08)
Others	-	-	0.37 (0.19)	2.56 (2.14)
Total	1.17 (0.66)	0.85 (0.51)	0.81 (0.43)	4.24 (2.27)
(twigs)				
S. arctica	-	-	-	4.02 (2.98)
S. glauca	1.62 (1.06)	0.09 (0.09)	-	-
S. reticulata	-	-	0.63 (0.63)	0.05 (0.05)
Others	-	-	0.77 (0.77)	6.59 (5.18)
Total	1.62 (1.06)	0.09 (0.09)	1.40 (1.40)	10.67 (5.79)
Graminoids				
Carex spp.	0.26 (0.13)	0.08 (0.06)	1.90 (0.61)	2.97 (0.58)
Festuca spp.	-	-	0.03 (0.03)	0.02 (0.02)
Luzula spp.	-	0.13 (0.07)	-	-
Poa arctica	+	0.16 (0.06)	-	-
Others	-	-	-	-
Total	0.27 (0.13)	0.36 (0.13)	1.90 (0.61)	2.99 (0.58)
Total Standing Crop	124.53 (26.80)	159.39 (30.39)	459.16 (52.69)	433.72 (33.76)

Table 2-4. continued

PLANT SPECIES	STAND NUMBER† S-1	2-5	2-1	2-4
Range Type	Mixed lichen dwarf shrub flats	Gravel ridges	Sedge moss stream bed	Sedge moss stream bed
Number of pellet-groups / 200m^2	0	25	38	5
Fruticose lichens				
Alectoria ochroleuca	16.46 (5.64)	0.91 (2.25)	0.62 (0.24)	0.02 (0.02)
Bryocaulon divergens	19.52 (3.18)	5.90 (1.51)	0.69 (0.34)	0.08 (0.05)
Cetraria islandica	25.36 (8.46)	3.45 (0.93)	27.44 (7.76)	4.49 (2.10)
Cetraria nivalis	53.09 (7.36)	12.98 (2.03)	11.85 (2.90)	2.43 (0.89)
Cladina mitis	26.21 (12.49)	0.81 (0.36)	0.09 (0.07)	-
Cladina rangiferina	9.09 (4.52)	0.92 (0.45)	7.83 (4.65)	4.15 (2.98)
Cladonia amourocrea	10.43 (3.38	0.09 (0.09)	0.09 (0.07)	0.02 (0.02)
Sphaerophous globosus	16.88 (5.07)	4.46 (1.73)	1.90 (0.82)	0.46 (0.34)
Others	23.93 (5.06)	5.73 (1.74)	5.16 (2.76)	0.21 (0.08)
Total	200.97 (30.21)	36.84 (5.46	59.78 (15.15)	11.87 (5.96)
Forbs				
Polygonum viviparum	+	-	1.27 (0.32)	0.23 (0.06)
Pyrola grandiflora	6.21 (3.55)	0.29 (0.21)	0.02 (0.02)	0.55 (0.43)
Saxifraga oppositifolia	5.18 (3.83)	0.07 (0.07)	-	-
S. tricuspidata	6.27 (2.17)	-	-	-
Others	6.75 (1.79)	1.09 (0.49)	0.50 (0.25)	0.77 (0.27)
Total	24.40 (5.61)	1.44 (0.66)	1.79 (0.41)	1.55 (0.59)
Dwarf Shrubs (current growth)				
Dryas integrifolia	0.30 (0.30)	27.38 (7.54)	14.33 (9.52)	1.28 (0.56)
Empetrum nigrum	-	-	-	-
Rhododendron lapponicum	-	-	5.64 (1.92)	4.15 (1.56)
Vaccinium uliginosum	-	5.47 (2.01)	2.32 (0.82)	8.21 (3.04)
Vaccinium vitis-idaee	-	2.11 (0.79)	1.02 (0.49)	0.44 (0.26)
Others	-	-	0.99 (0.63)	0.63 (0.35)
Total	0.30 (0.30)	34.95 (7.23)	24.30 (9.70)	14.72 (4.06)
(twigs)				
D. integrifolia	0.39 (0.39)	78.61 (29.85)	39.04 (21.52)	2.68 (1.14)
E, nigrum	-	-	-	-
R. lapponicum	-	-	13.55 (4.57)	10.00 (4.72)
V. uliginossum	-	22.45 (8.24)	7.85 (2.76)	23.14 (8.58)
V. vitis-idaee	-	0.86 (0.35)	0.45 (0.20)	-
Others	-	-	3.66 (2.62)	0.37 (0.20)
Total	0.39 (0.39)	101.92 (28.85)	64.55 (22.23)	62.48 (12.56)
Willows (current growth)				
Salix arctica	-	-	1.81 (1.02)	13.88 (3.75)
S. glauca	11.36 (6.55)	-	0.42 (0.42)	-
S. lanata	-	-	4.85 (1.53)	-
S. reticulata	-	-	11.64 (2.69)	3.90 (1.10)
Others	-	-	3.15 (3.15)	-
Total	11.36 (6.55)	-	23.69 (6.29)	17.78 (4.04)
(twigs)				
S. arctica	-	-		
S. glauca	14.14 (8.88)	-	2.31 (1.40)	21.00 (5.86)
S. lanata	-	-	14.00 (5.77)	-
S. reticulata	-	-	16.55 (4.45)	5.29 (1.39)
Others	-	-	-	-
Total	14.14 (8.88)	-	35.44 (9.09)	26.29 (6.38)
Graminoids				
Carex spp.	4.67 (1.84)	1.44 (0.45)	10.80 (1.91)	9.85 (2.08)
Festuca spp.	0.50 (0.26)	-	-	-
Luzula spp.	0.15 (0.10)	-	0.13 (0.13)	-
Poa arctica	0.44 (0.15)	-	-	-
Others	0.04 (0.04)	-	-	-
Total	5.80 (1.93)	1.44 (0.45)	10.93 (1.94)	9.85 (2.08)
Total Standing Crop	243.20 (29.96)	176.59 (36.32)	220.49 (30.26)	118.25 (20.55)

† First integer or letter in stand number denotes location of base camp (Figure 2-1). The second integer denotes the sample number.

Table 2-5. Mean biomass allocation (% of total weight ± SE) in shoots of *Salix glauca* and *S. lanata* in stands with different intensities of use by reindeer.

Sampling Period	25-27 July		2-4 August		26-28 August	
Relative Use†	H (B)	U (S)	M (C)	U (S)	H (D)	U (S)
Salix glauca						
Current growth	16.3[a] (1.7)	28.4[b] (1.5)	34.6 (2.1)	38.7 (2.3)	16.9[a] (2.0)	29.5[b] (1.9)
Live twigs	50.0 (4.3)	52.6 (1.7)	59.3[a] (2.1)	53.5[b] (1.9)	55.4 (2.2)	59.8 (1.8)
Flowers	0.6 (0.3)	2.4 (1.0)	2.7 (1.0)	2.2 (0.8)	0.0 (0.0)	0.9 (0.5)
Attached dead material	33.1[a] (5.1)	16.6[b] (2.2)	3.3 (0.4)	5.6 (1.1)	27.7[a] (2.8)	9.8[b] (1.3)
Salix lanata						
Current growth	12.5[a] (1.5)	26.6[b] (1.8)	35.0[a] (2.7)	23.2[b] (1.5)	13.0[a] (1.1)	22.6[b] (1.4)
Live twigs	53.9 (3.2)	58.5 (1.8)	52.4[a] (1.9)	63.4[b] (1.6)	67.4 (1.9)	63.8 (2.1)
Flowers	-	1.0 (0.5)	0.4 (0.3)	0.8 (0.3)	-	-
Attached dead material	33.5[a] (3.6)	13.9[b] (2.5)	12.1 (1.7)	12.6 (1.4)	19.6 (1.8)	13.6 (2.5)

† Sites were classified according to distribution of reindeer and pellet group densities in stands: H, high; M, moderate; U, unused. Letters in brackets denote location of camp (See Figure 2.1).

* One way ANOVA was restricted by species and sampling period; the meaningful comparison is between used and unused stands. Stands with different superscript letters are significantly different ($p < 0.05$).

Table 2-6. Nutritional characteristics of current growth in shoots of *Salix glauca* in stands with different intensities of use by reindeer.

Sampling Period	25-27 July		2-4 August		26-28 August	
Relative Use†	H (B)	U (S)	M (C)	U (S)	H (D)	U (S)
Total Cellulose (%)	24.7 (0.5)	22.9 (0.6)	29.0[a] (0.5)	23.9[b] (0.9)	26.2 (0.4)	24.6 (0.5)
Lignin (%)	16.1 (0.6)	14.6 (0.8)	28.7[a] (3.2)	12.8[b] (0.6)	19.3 (1.9)	20.5 (2.0)
Nitrogen (%)	3.10[a] (0.06)	2.46[b] (0.02)	2.55 (0.08)	2.33 (0.06)	2.51[a] (0.09)	2.11[b] (0.06)
Phosphorous (%)	0.26[a] (0.01)	0.17[b] (0.01)	0.14 (0.00)	0.14 (0.00)	0.23[a] (0.00)	0.14[b] (0.01)
Potassium (%)	1.46 (0.04)	1.61 (0.07)	1.69 (0.05)	1.76 (0.06)	1.47 (0.12)	1.52 (0.02)
Calcium (%)	1.33 (0.11)	0.88 (0.03)	1.25[a] (0.06)	0.97[b] (0.06)	1.56[a] (0.02)	1.20[b] (0.04)
Magnesium (%)	0.32 (0.03)	0.29 (0.04)	0.31 (0.01)	0.34 (0.01)	0.33 (0.01)	0.32 (0.03)

† Sites were classified according to distribution of reindeer and pellet group densities in stands: H, high; M, moderate; U, unused. Letters in brackets denote location of camp (See Figure 2.1).

* One way ANOVA was restricted by species and sampling period; the meaningful comparison is between used and unused stands. Stands with different superscript letters are significantly different ($p < 0.05$).

Table 2-7. Nutritional characteristics of current growth in shoots of *Salix lanata* in stands with different intensities of use by reindeer.

Sampling Period	25-27 July		2-4 August		26-28 August	
Relative Use†	H (B)	U (S)	M (C)	U (S)	H (D)	U (S)
Total Cellulose (%)	25.9 (0.7)	24.2 (0.3)	31.3[a] (1.2)	26.0[b] (0.2)	26.2 (0.6)	27.5 (0.7)
Lignin (%)	17.4 (4.0)	14.8 (1.0)	25.9 (2.2)	21.1 (3.8)	19.9 (2.1)	15.2 (1.1)
Nitrogen (%)	3.34[a] (0.02)	2.62[b] (0.02)	2.24 (0.15)	2.44 (0.05)	2.61[a] (0.08)	2.09[b] (0.05)
Phosphorous (%)	0.27[a] (0.01)	0.17[b] (0.01)	0.14 (0.01)	0.14 (0.01)	0.23[a] (0.01)	0.12[b] (0.01)
Potassium (%)	1.58 (0.04)	1.57 (0.11)	1.45[a] (0.02)	1.23[b] (0.06)	1.36 (0.04)	1.40 (0.06)
Calcium (%)	1.22 (0.05)	1.17 (0.09)	1.25 (0.05)	1.14 (0.09)	1.76[a] (0.02)	1.50[b] (0.07)
Magnesium (%)	0.30 (0.01)	0.30 (0.03)	0.38[a] (0.01)	0.48[b] (0.02)	0.31 (0.01)	0.29 (0.01)

† Sites were classified according to distribution of reindeer and pellet group densities in stands: H, high; M, moderate; U, unused. Letters in brackets denote location of camp (See Figure 2.1).

* One way ANOVA was restricted by species and sampling period; the meaningful comparison is between used and unused stands. Stands with different superscript letters are significantly different ($p < 0.05$).

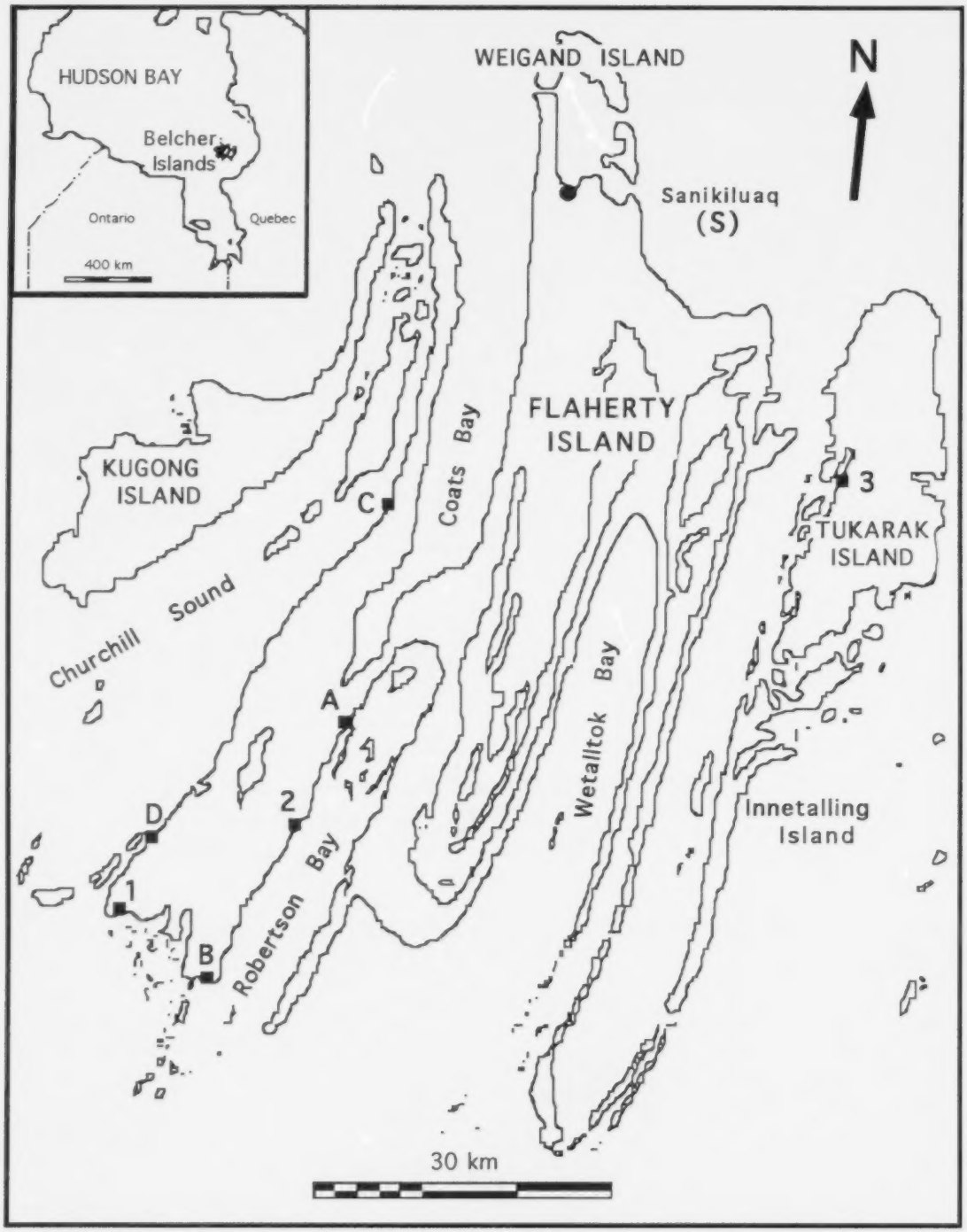


Figure 2-1. Locations of field camps on the Belcher Islands, Northwest Territories. Camps established in 1990 are represented by integers, and letters denote camp locations in 1991.

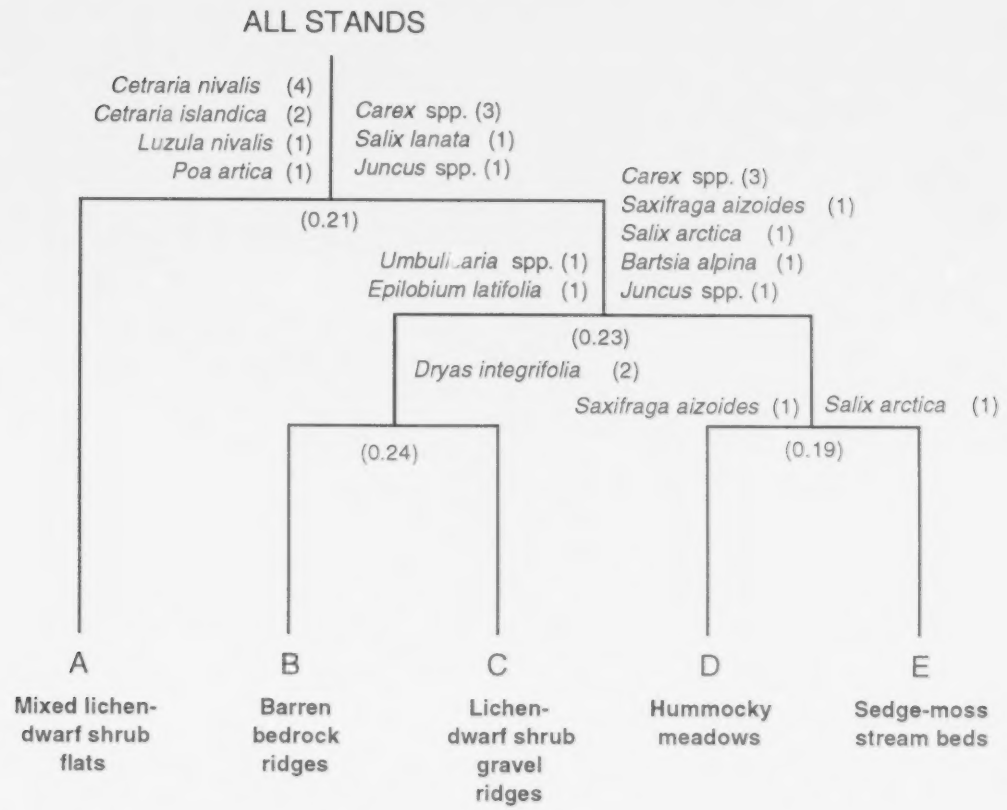


Figure 2-2. Dendrogram of TWINSPAN classification for stands of vegetation sampled on the Belcher Islands. Indicator species are shown on the right or left hand side of the dichotomy; integers in brackets indicate cover values on a scale of 1 to 5 using the following categories based on average cover values within a stand: 1, 0.01 - 1.9%; 2, 2 - 4.9%; 3, 5 - 9.9%; 4, 10 - 19.9%, 5, 20 - 100%. Eigenvalues are presented in brackets below each branch. Descriptions of community-types are based on Edmonds' (1979) range study.

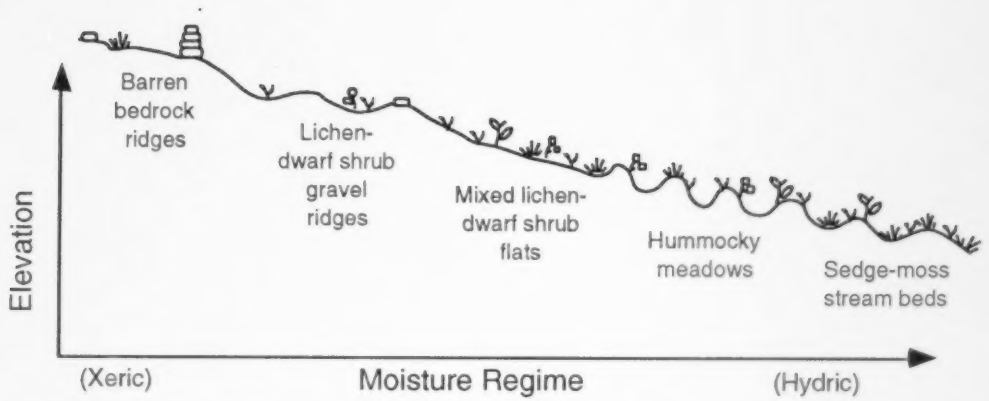


Figure 2-3. Typical caternary sequence of range communities on the Belcher Islands as related to elevation and moisture regime.

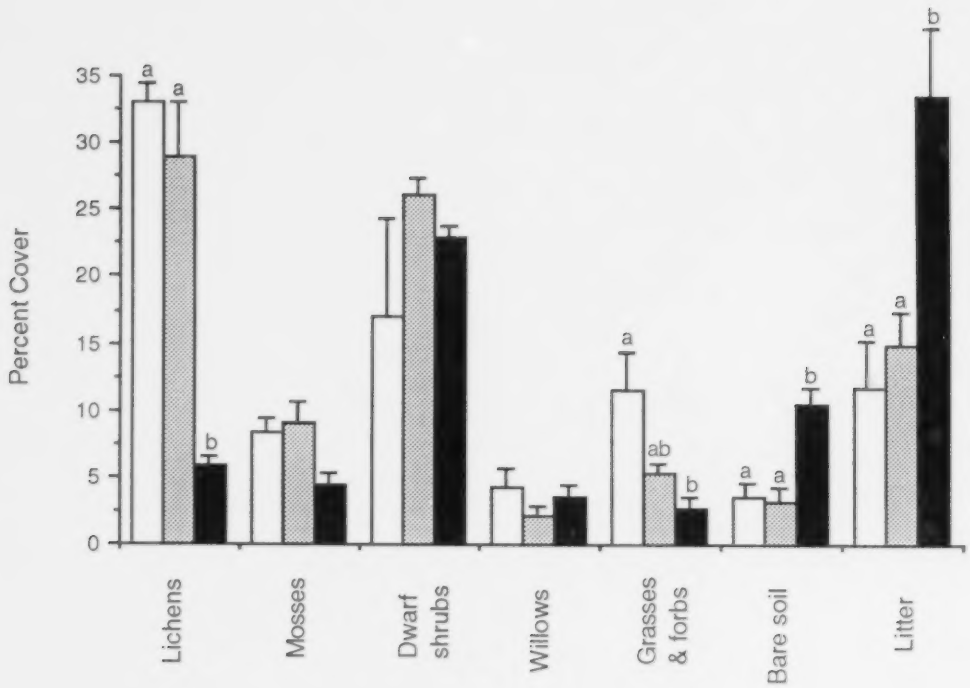


Figure 2-4. Comparative analysis of ground cover of plant growth forms in ungrazed (white bars) (n = 4), grazed (stippled) (n = 4), and heavily grazed (black bars) (n = 5) stands in the mixed lichen - dwarf shrub range type. Bars indicate mean cover values (± SE). Different letters within a growth form indicate significant differences ($p < 0.05$).

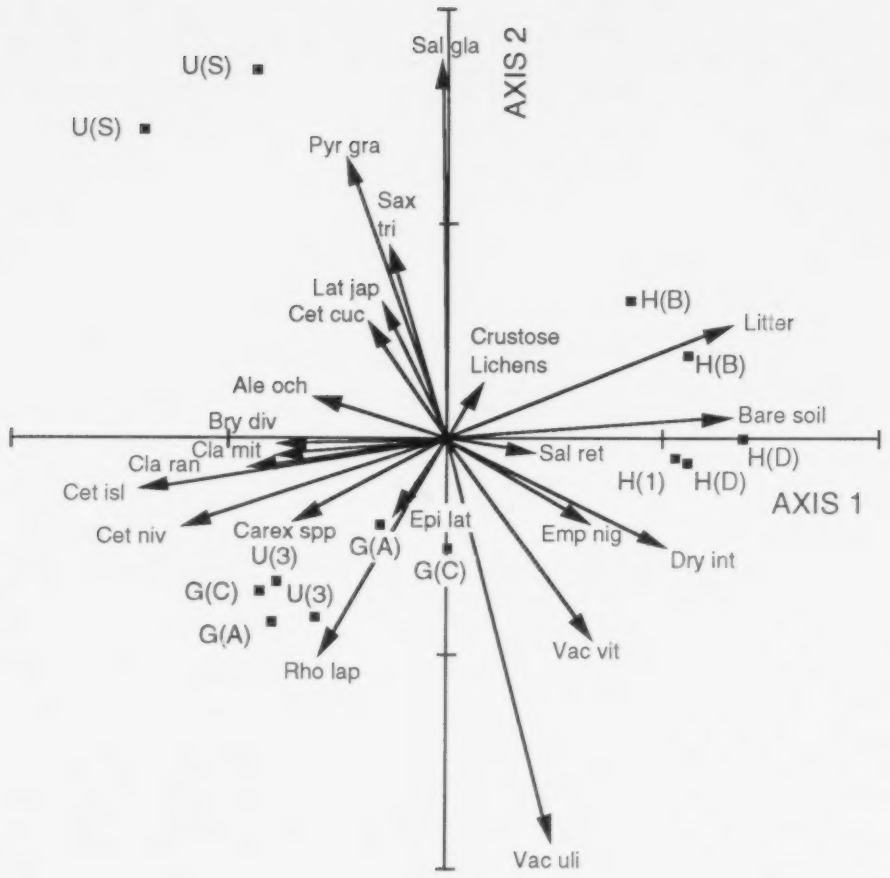


Figure 2-5. Ordination diagram based on a hybrid of redundancy analysis and principal components analysis on the floral composition of 13 stands in lichen-dominated range communities (community-type A; see Table 2-2 and Figure 2-2) on the Belcher Islands. The first axis is constrained by densities of reindeer pellet groups in a stand. The second axis displays residual variation in species composition of lichen-dominated communities, *i.e.*, variation not explained by pellet group densities. Species are represented by arrows and abbreviations are as follows: Ale och, *Alectoria ochroleuca*; Bry div, *Bryocaulon divergens*; Cet cuc, *Cetraria cucullata;* Cet niv, *C. nivalis;* Cet isl, *C. islandica;* Cla mit, *Cladina mitis;* Cla ran, *C. rangiferina;* Epi lat, *Epilobium latifolium;* Lat jap, *Lathyrus japonicus;* Pyr gra, *Pyrola grandiflora;* Sax tri, *Saxifraga tricuspidata;* Dry int, *Dryas integrifolia;* Emp nig, *Empetrum nigrum;* Rho lap, *Rhododendron lapponicum;* Sal gla, *Salix glauca;* Sal ret, *S. reticulata;* Vac uli, *Vaccinium uliginosum;* Vac vit, *V. vitis-idaea.* Stands are represented by solid squares and abbreviations are as follows: U, ungrazed; G, grazed, and H, heavily grazed; numbers or letters in brackets denotes location of base camp (see Figure 2.1). (λ_1 = 0.30, λ_2 = 0.25, scaling: 1 for species, and 1.75 for sites). For summary statistics see Table 2-3B.

Literature Cited

Adamczewski, J.Z., C.C. Gates, B.M. Soutar, and R.J. Hudson. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou *(Rangifer tarandus groenlandicus)* on Coats, Northwest Territories, Canada. Canadian Journal of Zoology. 66: 1986-1996.

Ahti, T., and J. Oksanen. 1990. Epigeic lichen communities of taiga and tundra regions. Vegetatio. 86: 39-70.

Anonymous 1983. Reindeer transplanted to the Belcher Islands 100 years after native caribou disappears. Caribou News. 3 (3): 11

Archer, S. and L. L. Tieszen. 1980. Growth and physiological responses of tundra plants to defoliation. Arctic and Alpine Research. 12: 531-552.

Arragutainaq, L., R.J. Hudson, and P. Poole. 1990. Reindeer surveys on the Belcher Islands. 1989-1990. Weasels Hunters and Trappers Association. Sanikiluaq, Northwest Territories. X0A-0W0. unpublished report. 19 pp.

Association of Official Analytical Chemists. 1984. Official methods of analysis. 14th ed. Association of Official Analytical Chemists, Washington, DC, USA.

Bergerud, A.T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. *In:* E. Reimers, E. Gaare, and S. Skjenneberg (eds). Proceedings of the 2nd International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet for vilt og ferzkvannsfisk. 556-581.

Bergerud, A.T. 1988. Caribou, wolves and man. Trends in Ecology and Evolution. 3: 68-72.

Bliss, L.C., J.B. Cragg, D.W. Heal, and J.J. Moore. (eds) Tundra Ecosystems: A Comparative Analysis. Cambridge University Press, Cambridge, England.

Bryant, J.P., F.S. Chapin III, and D.R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to herbivory. Oikos. 40: 357-368.

Bryant, J.P., P.B. Reichardt, and T.P. Clausen. 1992. Chemically mediated interactions between woody plants and browsing mammals. Journal of Range Management. 45: 18-24.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology. 51: 53-72

Caughley, G., and J.H. Lawton. 1981. Plant-herbivore systems. pp. 132-166. In: R.M. May, editor. Theoretical Ecology. Sinauer Associates Inc., Sunderland, Massachusetts, USA.

Chapin, F.S. III. 1980a. Nutrient allocation and responses to defoliation in tundra plants. Arctic and Alpine Research. 12: 553-563.

Chapin, F.S. III. 1980b. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics. 11: 233-260.

Chapin, F.S. III, and G.R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology. 66: 564-576.

Chapin, F.S. III, D.A. Johnson, and J.D. McKendrick. 1980. Seasonal movements of nutrients in plants of differing growth form in an Alaskan tudra ecosystem: implications for herbivory. Journal of Ecology. 68: 189-209.

Chapin, F.S. III, J.D. McKendrick, and D.A. Johnson. 1986. Seasonal changes in carbon fractions in Alaskan tundra plants of differing growth form: implications for herbivory. Journal of Ecology. 74: 707-731.

Chernov, Y. 1985. The Living Tundra. Cambridge University Press, Cambridge, England.

Crete, M., C. Morneau, and R. Nault. 1990. Biomasse et especes de lichens terrestres diponibles pour le caribou dans le nord du Quebec. Canadian Journal of Botany. 68: 2047-2053.

De Grosbois, T., G.P. Kershaw, and J.R. Eyton. 1991. The regrowth production and allocation of *Salix arbusculaoides* in three growinf seasons following right-of-way clearing. Canadian Journal of Forest Research. 21: 1171-1179.

Donaldson, J.A. 1986. Precambrian geology. pages 1-15 In I. P. Martini, editor. Canadian Inland Seas. Elsevier, New York, NY. Elsevier Oceanography Series No. 44.

Eberhardt, L.L., and J.M. Thomas. 1991. Designing environmental field studies. Ecological Monographs. 61: 53-73.

Edmonds, E.J. 1979. A study of reindeer *(Rangifer tarandus tarandus)* range on the Belcher Islands, Northwest Territories. Unpublished report. Canadian Wildlife Service. 37 pp.

Elton, C. 1965. Voles, Mice and Lemmings. Cramer-Weinheim, New York, New York, USA.

Ericsson, T. 1981. Effects of varied nitrogen stress on growth and nutrition in three *Salix* clones. Physiologia Plantarum. 51: 423-429.

Flaherty, R.J. 1918. The Belcher Islands of Hudson Bay: their discovery and exploration. The Geographical Review. 6: 433-458.

Fleck, S., and A. Gunn. 1982. Review of some ecological parameters that characterize the calving grounds of three barren-ground caribou herds of the Northwest Territories. Northwest Territories Wildlife Service. unpublished report.

Gaare, E., and T. Skogland. 1975. Wild reindeer food habits and range use in Hardangervidda. In F.E. Wielgolaski (ed.), *Fennoscandia Tundra Ecosystems.* Part 2. *Animals and Systems Analysis.* Ecological Studies, 17. Springer-Verlag, New York, New York, USA.

Goering, H.K., and P.J. Van Soest. 1970. Forage fiber analysis. Agriculture Handbook No. 379. Agriculture Research Service, U.S. Department of Agriculture. 20 pp.

Hale, M.E. 1979. How to know the lichens. Wm. C. Brown Company Publishers. Dubuque, Iowa, USA.

Helle, T., and J. Aspi. 1983. Effects of winter grazing by reindeer on vegetation. Oikos. 40: 337-343.

Henry, G.H.R. and A. Gunn. 1991. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic. 44: 38-42.

Hill, M.O. 1979. TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University Ithaca, New York, New York, USA.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs. 54: 187-211.

Jackson, G.D. 1960. Belcher Islands, Northwest Territories. Geological Survey of Canada. Paper 60-20. 13 pp.

Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren (eds.) 1987. Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen, the Netherlands.

Kightley, S.P.J., and R.I. Lewis Smith. 1976. The influence of reindeer on the vegetation of South Georgia: I. long term effects of unrestricted grazing and the establishment of exclosure experiments in various plant communities. British Antarctic Survey Bulletin. 44: 57-76.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management. 32: 350-367.

Klein, D.R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. Journal of Range Management. 40: 336-338

Kongsrude, J.L. 1988. Patterns of plant species richness on a polygonal peat plateau near Churchill, Manitoba. M.Sc. Thesis. York University. North York, Ontario. 137 pp.

Larouche, P. 1990. Winter offshore/onshore wind differences in Southeastern Hudson Bay. Arctic. 43: 55-59.

Leader-Williams, N. 1988. Reindeer on South Georgia: The Ecology of an Introduced Population. Cambridge University Press, Cambridge, England.

Lindsay, D.C. 1973. Effects of reindeer on plant communities in the Royal Bay area of South Georgia. British Antarctic Survey Bulletin. 35: 101-109.

Machinski, J., and T.G. Whitham. 1989. The contiuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. American Naturalist. 134: 1-19.

Macnab, J. 1985. Carrying capacity and related slippery shibboleths. Wildlife Society Bulletin. 13: 403-410.

Maxwell, J.B. 1986. A climate overview of the Canadian inland seas. pages 79-100, In I. P. Martini, editor. Canadian Inland Seas. Elsevier, New York, NY. Elsevier Oceanography Series No. 44.

Messier, F., J. Huot, D. Le Henaff, and S. Luttich. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic. 41: 279-287.

McNaughton, S.J. 1983. Compensatory plant growth as a reponse to herbivory. Oikos. 40: 329-336.

Mould, E.D. and C.T. Robbins. 1981. Evaluation of detergent analysis in estimating nutritional value of browse. Journal of Wildlife Management. 45: 937-947.

Nicholson, F.H. 1976. Patterned ground formation and description as suggested by low arctic and subarctic examples. Arctic and Alpine Research. 8: 329-342.

Noy-Meir, I. 1973. Data transformation in ecological ordination. I. Some advantages of non-centering. Journal of Ecology. 61: 329-341.

Noy-Meir, I., and R.H. Whittaker. 1977. Continuous multivariate methods in community analysis: some problems and developments. Vegetatio. 33: 79-98.

Noy-Meir, I., D. Walker, and W.T. Williams. 1975. Data transformations in ecological ordination. II. On the meaning of data standardization. Journal of Ecology. 63: 779-800.

Ouellet, J.P. 1992. Ecology on an introduced caribou population on Southampton Island, N.W.T., Canada. Ph.D. Thesis. University of Alberta. Edmonton, Alberta. 123 pp.

Palmer, L.J. and C.H. Rouse. 1945. Study of the Alaska tundra with reference to its reactions to reindeer and other grazing. U.S. Fish and Wildlife Service Research Report. 10: 48 pp.

Parker, G.R. 1975. An investigation of caribou range on Southampton Island, Northwest Territories. Canadian Wildlife Service Report Series. No. 33. 83 pp.

Pegau, R.E. 1968. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. Arctic. 21: 255-259.

Pegau, R.E. 1970a. Effect of reindeer trampling and grazing on lichens. Journal of Range Mangement. 23: 95-97.

Pegau, R.E. 1970b. Succession in two exclosures near Unalakleet, Alaska. Canadian Field Naturalist. 84: 175-177.

Porsild, A.E., and W.J. Cody. Vascular plants of Continental Northwest Territories, Canada. National Museum of Natural Sciences. Ottawa, Ontario. 667 pp.

Ricketts, B.D. and J.A. Donaldson. 1981. Sedimentary history of the Belcher Group of Hudson Bay. Geologic Survey Paper 81-10: 235-254.

Ricketts, B.D. and J.A. Donaldson. 1989. Stromolite reef development on a mud-dominated platform in the middle Precambrian Belcher group of Hudson Bay. In Reefs, Canada and Adjacent Area. H. H. G. Geldsetzer, N. P. James and G. E. Tebutt, editors, Canadian Society of Petroleum Geologist Memoir. 13: 113-119.

Ricketts. B.D., M.J. Ware, and J.A. Donaldson. 1982. Volcaniclastic rocks and volcaniclastic facies in the Middle Precambrian (Aphebian) Belcher Group, Northwest Territories, Canada. Canadian Journal of Earth Science. 19: 1275-1294.

Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. IUCN Publication New Series. No. 4: 261-273.

Scheffer, V.B. 1951. The rise and fall of a reindeer herd. Scientific Monthly. 73: 356-362.

Scotter, G.W. 1964. Effects of forest fires on winter range of barren-ground caribou in Northern Saskatchewan. Canadian Wildlife Service. Wildlife Management Bulletin Series 1. No. 18. 111 pp.

Shaver, G.R., and F.S. Chapin III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology. 61: 662-675.

Simon, M., L. Zsuffa, and D. Burgess. 1990 Variation in N, P, K status and N efficiency in some North American willows. Canadian Journal of Forest Research. 20: 1888-1893.

Skogland, T. 1984. Wild reindeer foraging-niche organization. Holarctic Ecology. 7: 345-379.

Skogland, T. 1988. Tooth wear by food limitation and its life history consequences in wild reindeer. Oikos. 51: 238-242.

Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd. Oecologia. 84: 442-450.

Skunke, F. 1969. Reindeer ecology and managment in Sweden. University of Alaska Biological Papers. No. 8. 82 pp.

Swanson, J.D., and M.H.W. Barker. 1991. Assessment of Alaska reindeer populations and range conditions. Rangifer. 12: 33-43.

ter Braak, C.J.F. 1983. Principal components biplots and alpha and beta diversity. Ecology. 64: 454-462.

ter Braak, C.J.F. 1992. CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondance analysis, principal components analysis and redundancy analysis (version 3.10). Agricultural Mathematics Group, Wageningen, the Netherlands.

Thing, H. 1984. Feeding ecology of the West Greenland caribou *(Rangifer tarandus groenlandicus)* in the Sisimiut-Kangerlussuaq region. Danish Review of Game Biology. 12 (3). 53 pp.

Thomas, D.C. and E.J. Edmonds. 1984. Competition between caribou and muskoxen, Melville Island, N. W. T., Canada. Biological Papers of the University of Alaska. Special Report No. 4: 93-100.

Tyler, N.J.C. 1987. Natural limitation of the abundance of the High Arctic Svalbard reindeer. Ph.D. Thesis. University of Cambridge. Cambridge, England. 327 pp.

Vitt, D.H., J.E. Marsh, and R.B. Bovey. 1988. Mosses, lichens and ferns of northwest North America. Lone Pine. Edmonton, Alberta, Canada.

Webster, D.B. 1992. Viewpoint: replication, randomization, and statistics in range research. Journal of Range Management. 45: 285-290.

White, R.G., and J. Trudell. 1980. Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research. 12: 511-529.

Wilkinson, L., M. Hill, S. Miceli, P. Howe, and E. Vang. 1992. SYSTAT: Version 5.2 Edition. Evanston, Ilinois, USA.

Wilson, A.D., and N.D. Macleod. 1991. Overgrazing: present or absent? Journal or Range Management. 44: 475-482.

Wynne, F.E., and W.C. Steere. 1943. The bryophyte flora of the east coast of Hudson Bay. The Bryologist. 46: 73-87.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inglewood Cliffs, New Jersey, USA.

Chapter 3

Seasonal range use and diets, and late winter body condition of an increasing population of introduced reindeer

Introduction

Caribou *(Rangifer tarandus groenlandicus)* depend mostly on forage to meet their bioenergetic requirements for maintenance, activity, and reproduction during winter; the relative contribution of body reserves of fat and protein accumulated over summer is comparatively small (Adamczewski *et al.* 1993). Thus, in the absence of predators, populations of reindeer and caribou may be limited by forage availability in winter (Leader Williams 1988, Tyler 1987, Skogland 1985, 1990, Adamczewski *et al.* 1988). Winter forage availability is directly affected by two discrete but interactive factors: density-independent snow conditions (depth and hardness of the snowpack), and density-dependent range conditions (degree to which grazing, browsing, and/or trampling have affected quantity and quality of forage). The limiting effects of snow cover on forage availability have been well demonstrated (Pruitt 1959, Lappiere and Lent 1977, Skogland 1978, Adamczsewski *et al.* 1988, Collins and Smith 1991). In the most extreme case, forage may be totally inaccessible due to icing conditions and animals either disperse (Miller *et al.* 1977) or starve (Scheffer 1951, Klein 1968). A good demonstration of the effect of range condition on winter forage availability and thus growth and body condition of *Rangifer* comes from Ouellet's (1992) comparative study of Southampton Island caribou with related animals on Coats Island (see Adamczewski *et al.* 1988). On Southampton Island, per capita food availability was greater and introduced caribou increased rapidly and steadily; male and female caribou were in exceptional physical condition (Ouellet 1992). On neighboring Coats Island per capita food availability was substantially less (Adamczewski *et al.* 1988). The population has fluctuated due to heavy calf mortality in years with adverse snow conditions (Gates *et al.* 1986). Given that the two islands are in close proximity to each other and experience relatively similar weather conditions, Ouellet (1992) suggested that growth of northern predator-free populations of *Rangifer* may be predicted by winter food availability which is influenced by climatic conditions and grazing.

Reindeer *(R. t. tarandus)* were introduced on the Belcher Islands in March 1978, and have already overgrazed portions of their range (Chapter 2). Thus, my objective was to determine whether reindeer have been negatively affected by forage availability in late winter - a critical time of the year in the ecology of *Rangifer*. Based on previous studies, I asserted that reduced availability of winter forage (due to either overgrazing of lichen communities) would express itself in one or more of the following ways: 1) reindeer would change their grazing habits by foraging in less favorable habitats as lichen range was depleted (Staaland *et al.* 1993), 2) reindeer would replace lichens in their winter diet with other plants such as mosses, graminoids, and dwarf shrubs as availability of lichens decreased (Skogland 1984, 1985, Baskin 1989), accompanying this change in diet composition would be an increase in crude fiber of the diet (Adamcweski *et al.* 1988), and 3) body size (Reimers 1971, 1983a, Skogland 1983) and energy reserves of adult females would decline. Body reserves of fat and protein are good indicators of nutritional status and fertility in adult female reindeer and caribou (Dauphine 1976, Parker 1981, Thomas 1982, Reimers 1983b, Adamczewski *et al.* 1987b). I collected data on late winter body condition, and seasonal range and diet selection to test this assertion.

Methods and Materials

Study population

The Belcher Islands are located in the southeast part of Hudson Bay, approximately 110 km off the coast of Quebec (Figure 2-1). Climate and vegetation are characteristic of low arctic tundra. For a detailed description of the study area see Chapter 2.

In March 1978, the Government of the Northwest Territories purchased sixty reindeer *(R. t. tarandus)* from the Mackenzie Delta herd near Tuktoyuktuk and introduced them onto the Belcher Islands, approximately 100 years since caribou were last found there. Thus, Belcher Island reindeer are descendants of Mackenzie Delta reindeer, which in turn are related to the animals that were originally bought in Siberia and transported to Alaska (see Scotter 1972, 1978, Godkin 1986b).

Range use

I used counts of pellet-groups within belt transects (2 m x 100 m) as an index of relative use by reindeer (see Neff 1968). All pellet transects were sampled in conjunction with vegetation sampling (Chapter 2) and were located within hiking distance of base camps established over two summers of field work (1990-91) (Figure 2-1).

I defined a pellet-group as an aggregation of 10 or more individual fecal pellets. Pellet-groups were classified as winter or summer type; pellets dropped in winter were a loose aggregation of hard, spheroid pellets while summer pellets were amorphous and compressed together. I randomly located transects within distinct range communities (Chapter 2) and counted all pellet-groups within the 200 m^2 strip. Pellet-groups occurring on the boundary of the transect were counted if more than half of the group lay within. A toss of a coin was used to determine whether those pellet-groups lying exactly on the transect boundary were included or not.

Diet composition and nutrition

I determined diet composition of reindeer in summer (July - August) and late winter (March) from fecal and rumen samples respectively. I collected freshly dropped feces from reindeer in summer (1990 - 91) and air-dried all samples in the field. Upon returning to the laboratory I pooled three pellets from each pellet group into a composite sample and ground the fecal material with a Wiley mill (No. 20 mesh screen). Those samples were sent to the Composition Analysis Laboratory in Fort Collins, Colorado, where experienced technicians used the microhistological technique to estimate mean

relative density of plant cuticular fragments (Sparks and Malechek 1968). Composition was estimated from four slides per sample at 20 fields per slide.

I used both the microhistological technique (Sparks and Malechek 1968) and point estimate technique (Chamrad and Box 1964) to estimate winter diet composition from rumen samples. Rumen samples were collected concurrently during body condition surveys in March 1989 and 1991. In the field, rumen contents were mixed thoroughly and a 1 liter sample was collected and quickly frozen. Rumen samples were thawed in the laboratory at the University of Alberta, whereupon I combined 10 ml from each individual sample to make a composite sample for each year. I washed each composite sample through a series of four screens (2.0, 0.8, 0.4, and 0.1 mm respectively). Material from each screen was then recombined, air-dried, and ground using a Wiley mill to pass through a No. 20 mesh screen. These composite samples were also sent to the Composition Analysis Laboratory for microhistological analysis.

I washed remaining rumen samples individually and identified plant material retained on the 2 mm screen. I spread plant material evenly over the bottom of an enamel tray (17 x 28 cm) and estimated composition using a point frame. A 5-pin point frame was advanced across the tray at 1 cm intervals for a total of 100 points per tray. Composition of each rumen sample was estimated twice for a sampling intensity of 200 points per sample.

Quality of late winter diets was assessed by proximate analysis of washed rumen material (Klein 1962, Crete *et al.* 1990). I used the Kjeldahl method (A.A.O.C. 1984) to determine nitrogen content, and the neutral (NDF) and acid detergent method (ADF), and 72% H_2SO_4 lignin technique to measure fiber content (Goering and Van Soest 1970).

Body condition

In March 1989 and 1990, the Weasels' Hunters and Trappers Association (HTA) conducted body condition surveys of reindeer in association with their late winter hunts (Arragutainaq *et al.* 1990). Ten reindeer were collected during each survey. In March 1991, I accompanied hunters on the body condition survey. We collected 10 reindeer and recorded the following condition parameters: liveweight, depth of back fat, length and weight of the femur, and weight of the gastrocnemius muscle. I used mass of gastrocnemius (including the flexor digitalis) and femur to predict carcass dissectible muscle and bone based on regression equations determined by Ringberg *et al.* (1981) for Alaskan reindeer. Depth of back fat was used to estimate carcass dissectible fat using Reimers and Ringberg's (1983) equation for Svalbard reindeer. I classified reindeer as

adults (age > 29 months) and subadults (12 < age < 29 months) according to tooth eruption patterns (see Miller 1974). However, jaw bones from reindeer in 1989 were mislabeled and jaws from the 1990 survey were unavailable. Thus, I classified those female reindeer as adult and subadult based on relative body size; animals with liveweights less than 90 kg were considered subadults. Reindeer collected in March 1989 and 1990 were located on the southwest arm of Flaherty Island and in March 1991 reindeer were collected from south-central Flaherty Island.

Data analyses

The natural log of the population counts of reindeer were plotted against time to determine the observed rate of increase (Caughley 1977). Body condition indices for adult female and subadult male reindeer were compared between years using ANOVA. Inadequate sample sizes precluded comparisons of body condition data for subadult females.

Counts of pellet-groups have been well described by the negative binomial distribution (Bowden *et al.* 1969, McConnell and Smith 1970, Stormer *et al.* 1977, White and Eberhardt 1985). The negative binomial distribution described my observed counts of pellet-groups (Chi-Square goodness-of-fit test; Krebs 1989) but a logarithmic transformation (Elliot 1977) did not normalize the data. Due to missing cells, small sample sizes, and absence of pellet-groups in many transects at Camps 1, 2, 3, and S (Table 3-1), I restricted further analyses to pellet group data collected at Camps A, B, C, and D. I used Kolmogorov-Smirnov two sample tests (Sokal and Rohlf 1981) to compare frequency distributions of pellet-group counts among camp locations. Based on those results (Table 3-1), I pooled pellet data from Camps A and C, and Camps B and D into "low density" and "high density" areas respectively.

I used one-way ANOVAs to detect differences in plant categories of rumen contents between years as estimated by the point estimate technique. The 95% probability level ($p \leq 0.05$) was used to determine significant differences. Analyses were conducted using the SYSTAT software package (Wilkinson *et al.* 1990) and means are presented with standard errors (SE) unless otherwise noted.

Results

Population dynamics

The introduced reindeer herd on the Belchers consisted of 50 adult females and 10 adult males (Popko 1979). Upon release, reindeer scattered and dispersed throughout Flaherty and Weigand Island (Edmonds 1979). A snowmobile ground survey conducted in June 1978 indicated that spring concentrations of reindeer were on Weigand Island and on Flaherty Island north of Kasegalik Lake (Figure 2-1) (Popko 1979). The following summer, Popko (1979) conducted an aerial survey of the Belchers and counted only 22 reindeer. However, based on hunter information, he estimated the population at 109 animals. Reindeer were observed throughout Flaherty Island with tracks seen on Howard Peninsula, Mukpollo Peninsula, northeast of Kasegalik Lake, and in the South Camp area (Popko 1979). Reindeer had also been sighted on Weigand, Johnson, southeast Kugong, Tukarak, and the Baker's Dozen Islands. In March 1982, Ferguson (1985) counted 222 reindeer during an aerial strip survey of the Belchers and estimated the population at 287 $\pm$ 110 animals. He observed four groups of 169, 26, 23, and 4 reindeer respectively. The two largest aggregations were located on southwest Flaherty Island, whereas the smaller groups were observed on Tukarak Island. "Local residents reported that large groups of reindeer had occupied southwestern Flaherty during winters from 1980 - 1985" (p. 10; Ferguson 1985). In March 1989 and 1990, the Weasels' HTA conducted both aerial photographic surveys and snowmobile ground surveys of reindeer (Arragutainaq *et al.* 1990). Counts of reindeer in 1989 and 1990 based on aerial photographic surveys were 479 and 561 respectively. In both years, counts based on snowmobile ground surveys differed by less than 4% of counts recorded using aerial photographic surveys. This indicated similar accuracies for the two methods (Arragutainaq *et al.* 1990). Single large aggregations of reindeer (103 - 375 animals) were consistently observed in the southwest arm of Flaherty Island. Smaller aggregations of reindeer (2 - 64 animals) were observed commonly on Kugong, Tukarak, and Inetalling Islands (Arragutainaq *et al.* 1990).

Surveys of reindeer on the Belcher Islands indicate that this population increased rapidly since the introduction of 60 animals in 1978 (Figure 3-1. A). The observed rate of increase (r) (Caughley 1977) based on all four population counts from 1978 to 1990 was 0.20 (Figure 3-1. B). However, population growth likely varied during this period because reindeer were first harvested (two females and six males) by local hunters in January 1983. In January 1984, the Weasels' HTA approved an annual quota equivalent to 50% of the estimated number of yearlings (Ferguson 1985). From 1978

to 1982 (pre-hunting), the population increased at an observed rate (r) of 0.39. Heard (1990) adjusted for distorted age and sex ratios of the introduced herd and calculated an intrinsic rate of increase (r_m) of 0.28 for Belcher Island reindeer. Subsequently between 1982 and 1990, r apparently declined to 0.08 as the population was stabilized by harvest.

Range use

A total of 144 pellet transects were sampled from eight base camp locations (Figure 2-1). Inadequate sample sizes of pellet-group transects in summer 1990 (*i.e.*, Camps 1, 2, and 3) preclude those data from statistical comparisons. Rather, mean numbers of pellet-groups counted within transects are presented in Table 3-1. There were no pellets detected in transects sampled within the vicinity of Sanikiluaq (*i.e.*, Camp S) (Table 3-1).

Distributions of pellet-groups at Camps "A" and "C" were not significantly different (Table 3-2). These two locations represented areas of relatively low reindeer densities. Similarly, distributions of pellet-groups at Camps "B" and "D" were not significantly different (Table 3-2), and represented areas of high reindeer densities. Pellet-group data from high density areas showed that greatest densities of winter type pellets occurred in the "mixed lichen-dwarf shrub flats" range type (Figure 3-2). Winter type pellet-groups were found in the other range communities but at substantially lower densities. Summer type pellets in the high density areas were most abundant in the "mixed lichen-dwarf shrub flats" and "sedge moss stream beds" and were found at relatively higher densities and throughout a broader spectrum of range communities than winter type pellets (Figure 3-2).

Diet composition and nutrition

Summer diet of reindeer on the Belcher Islands consisted primarily of willows. Willows accounted for greater than 97%, and graminoids and lichens represented less than 3% of plant fragments identified in fecal pellets (Table 3-3). While in the field, I also observed reindeer feeding on the flowering parts of *Epilobium latifolium*, and on one occasion a small group foraged extensively on mushrooms. Along stream and lake margins, forbs such as *Hipparis vulgaris, Menyanthes trifoliata, Potentilla palustris,* and various sedges such as *Carex aquatalis, Eriophorum callitrix* and *E. angustifolium* were grazed by reindeer.

Relative abundance of plants in winter rumens varied between the two methods. Winter diet composition as estimated by the microhistological technique on composite rumen samples suggested that lichens accounted for greater than 51% of rumen contents

and were the most important forage to reindeer. Graminoids, shrubs, and mosses were second, third and least abundant respectively (Table 3-4). Graminoids and mosses were relatively similar in abundance between years; mean values were 20.1% and 10.1% respectively. However, abundance of lichens and shrubs varied substantially between years. Lichens were more abundant in 1990 (61.2%) than in 1989 (51.6%), whereas shrubs were more abundant in 1989 (20.5%) than in 1990 (6.4%) (Table 3-4). Forbs were not detected in winter rumen samples in either year.

Conversely, the point estimate technique ranked graminoids as most abundant followed by dwarf shrubs, lichens, mosses and forbs respectively (Table 3-4). Leaves and twigs of *Salix* spp. represented over 55% of the shrub component in rumens (Table 3-5). *Vaccinium uliginosum* and *V. vitis-idaea* constituted an additional 35-36%. *Dryas integrifolia, Empetrum nigrum,* and *Rhododendron lapponicum* accounted for the remaining 9% (Table 3-5). Abundance of shrubs was not significantly different between years. However, proportion of leaves of *Vaccinium* spp. were significantly lower in March 1991 (Table 3-4). Mean proportion of lichens was significantly lower in rumen samples collected in 1989. This difference was apparent for all groups of lichens (Table 3-4). Lichens of the genus *Cladina* and *Cetraria* were the most common lichens identified in rumens (Table 3-4 and 3-5). Other lichens found in rumens were *Alectoria ochroleuca, Bryocaulon divergens, Thamnolia vermicularis, Cladonia* spp. and a foliose lichen (likely a species of *Umbilicaria*) (Table 3-5).

Abundance of graminoids and shrubs was consistently higher when rumen contents were determined by the point estimate technique compared to the microhistological technique. In contrast, the point estimate technique consistently underestimated abundance of lichens. Estimates of moss abundance were similar between both methods (Table 3-4).

Levels of nitrogen, acid detergent fiber, and lignin/cutin in washed rumen samples were significantly greater in 1989 compared to 1990 (Table 3-6).

Body condition

Average liveweights of adult female reindeer were significantly different between years. Liveweights in 1990 (98.8 $\pm$ 2.4 kg) were significantly greater than weights in 1989 (95.8 $\pm$ 2.4) (Table 3-7). Liveweights for subadult females and males were not significantly different between years; mean values over all three collections were 83.0 $\pm$ 3.2 kg, and 83.8 $\pm$ 2.9 kg respectively. There were no significant differences in other condition indices between years in either adult females or subadult males (Table 3-7).

Mean values for predicted carcass muscle, bone, and fat in adult cows was 38.9 $\pm$ 0.9 kg, 9.3 $\pm$ 0.2 kg, and 5.0 $\pm$ 0.7 kg respectively. Average predicted carcass muscle and bone mass for subadult females was 35.0 $\pm$ 2.1 kg and 8.9 $\pm$ 0.5 kg respectively. For subadult males mean predicted carcass muscle and bone mass were 39.8 $\pm$ 1.9 kg and 9.4 $\pm$ 0.4 kg respectively. Mean predicted carcass dissectible fat for subadult females was 3.9 $\pm$ 0.8 kg, whereas subadult males averaged 2.1 $\pm$ 1.2 mm.

Discussion

Population Dynamics

Surveys of BI reindeer suggest that hunting may have had an effect on population growth. Upon introduction in March 1978, reindeer increased from 60 to an estimated 287 animals in 1982 ($r = 0.39$, $r_m = 0.28$, Heard 1990). Subsequent surveys in March 1989 and 1990 indicated a decline in observed rate of increase relative to the 1982 population estimate ($r = 0.08$). This decline was concomitant with the initiation of hunting in January 1983 and the establishment of a harvesting scheme in 1984, whereby 50% of the estimated number of yearlings were killed annually (Ferguson 1985).

Twinning may occur in reindeer (Godkin 1986a) and has important implications for population dynamics. Reindeer may also become pregnant as calves (4 months old) (Reimers 1983). Hunters on the Belcher Islands have reported twinning but no occurrences of pregnant calves; this merits further investigation on productivity and recruitment in this reindeer population.

Range use

Pellet-group counts may be interpreted as indicating actual or relative numbers of ungulates, or their time of use in a given area (Neff 1968). My pellet-group data clearly showed that the southwest region of Flaherty Island had the highest relative densities of reindeer fecal pellets. I argue that those data reflect both high relative densities and a long history of use by BI reindeer. Aerial and ground surveys (Ferguson 1985, and Arragutainaq *et al.* 1990) showed that the largest groups of reindeer, *i.e.*, greater than 100, were consistently observed in the southwest region of Flaherty Island. Hunters and local residents (Ferguson 1985) reported that reindeer have occupied that region of the Belchers since 1980. Thus, it is apparent that a large proportion of the BI reindeer population have shown philopatry to the southwest region of Flaherty Island since 1980.

Why do reindeer occupy the southwest region of Flaherty Island? Reasons for the observed distribution of reindeer on the Belchers, and their apparent philopatry to the southwest region of Flaherty Island may be related to food abundance, environmental (climatic) conditions, and/or levels of human-caused harassment. However, if food abundance were the most important factor influencing distribution and range use by reindeer, one would expect to observe extensive use of productive lichen range (Edmonds 1979) in the northern parts of Tukarak and Flaherty Islands, and also on Kugong Island.

Although lichen range is relatively abundant on Kugong Island (Edmonds 1979), local Inuit suggest that reindeer do not remain there because the topography does not provide shelter from the wind in winter (M. Fleming unpub. data). Rather, residents suggest that a relative lack of human-caused disturbance and shelter from prevailing winds are the reasons for the present distribution of reindeer occurring principally in the southwest, south-central, and southeast areas of Flaherty Island (M. Fleming unpub. data). They believe that reindeer do not travel further north on Flaherty Island or establish a larger herd on Tukarak Island because of vehicular and aircraft noise respectively (M. Fleming unpub. data). It appears that Belcher Island reindeer are similar to Svalbard reindeer in the respect that animals confine their activities within relatively small areas and display long-term fidelity to particular regions (Tyler and Øritsland 1989).

The net effect of continual occupation by large numbers of reindeer in southwest Flaherty is overgrazing of lichen and willow dominated range communities (Chapter 2). As an area becomes overutilized, reindeer will be forced to disperse into unfamiliar areas where food is more abundant. If hunting and human-caused harassment are factors that affect range use and distribution of reindeer, restriction to a relatively small home range which becomes progressively overgrazed has implications for the productivity of the population. Therefore, a better understanding of seasonal movements and home range size of reindeer relative to range conditions and human land-use practices is crucial for management of this population.

In southwest Flaherty Island, the distribution of "winter" and "summer" type pellet-groups suggest that reindeer use the "mixed lichen-dwarf shrub flats" most in winter, whereas high densities of "summer" type feces are found in "mixed lichen-dwarf shrub flats" and "sedge moss stream beds." Although an assessment of range use based on pellet-group counts does not represent an unambiguous interpretation of habitat use (see Fuller 1991) because it is based on an assumption that defecation rates are consistent and equivalent to time spent within a habitat (Collins and Urness 1981, Rowland *et al.* 1984), results from the diet analysis support my assertion that those range communities are preferentially used in winter and summer. Lichens and willows are the dominant forage types consumed by reindeer in winter and summer respectively. It is reasonable to believe that snow conditions in winter (see Appendix 2) may restrict forage availability to lichen-dominated communities (see Adamczewski *et al.* 1988, Collins and Smith 1991). The fact that lichen and willow-dominated range communities were the first to be negatively affected (Chapter 2) further corroborates importance of those habitats to reindeer.

Diet composition and nutrition

A major source of bias in determining diet composition of ruminants from fecal or rumen samples arises from differential rates of digestion and fragmentation of various plant types (Dearden *et al.* 1975, Gaare *et al.* 1977, Vavra and Holechek 1980, Holechek *et al.* 1982). Thus, in studies on food habits of *Rangifer,* consumption of lichens, green forbs, and mushrooms is usually underestimated or not detected while intake of evergreen shrubs, and mosses is overestimated (Bergerud and Russell 1964, Scotter 1966, Boertje 1984, Boertje *et al.* 1985, Thomas and Hervieux 1986, Thomas and Barry 1991). Despite my observations of reindeer foraging on forbs and mushrooms, those plant types were not detected in fecal samples. Therefore, abundance of willows was overestimated. Nevertheless, microhistological analysis of fecal pellets clearly indicated that willows were the dominant dietary component in summer for Belcher Island reindeer.

Extensive use of willows and other dwarf shrubs in summer by *Rangifer* is common (Thompson and McCourt 1981, Boertje 1981, Crete *et al.* 1990), and abundance within the diet may vary latitudinally (Klein 1986, Jefferies *et al.* 1992). Heavy consumption of willows by Belcher Island reindeer corresponds closely to summer diets of Peary caribou *(R.t. pearyi)* in the High Arctic, and caribou on Coats Island in northern Hudson Bay. Parker (1978) found that willow comprised 82, 89, and 64% of plant fragments in fecal samples of Peary caribou collected in July on Axel Heiberg, Melville, and Bathurst Island respectively. On Coats Island, willows accounted for approximately 75-90% of rumen contents of caribou collected in July and August (from Figure 5 in Adamczweski *et al.* 1988). Heavy use of willows in summer may be related to protein requirements of calves during early lactation and restoration of body musculature (Adamczweski *et al.* 1988, Crete *et al.* 1990).

Based on results from the microhistological technique, lichens represent the largest component (> 50% of rumen contents) in the winter diet of Belcher Island reindeer. Similarly, Thomas and Barry (1991) found that lichens comprised 91, 87, and 79% of rumen and fecal samples of barren ground caribou collected in late winter from the Beverly herd on forest, forest-tundra, and tundra habitat respectively. Boertje (1984) estimated that lichens represented 62% of the diet in adult female caribou in Alaska. However, on Coats Island where lichen range has been overgrazed, rumens of caribou consisted of approximately 5-20% lichens in late winter (from Figure 5 in Adamczewski *et al.* 1988).

Regardless of technique, lichens were more abundant in the rumens of reindeer collected in March 1991 than in March 1989. This difference in lichen content between years and relative abundance of *Empetrum nigrum* (an unpreferred species) in 1989, may indicate that range conditions in southwest Flaherty Island were poorer than in south-central Flaherty Island or that snow conditions made foraging more difficult in 1989. Diet quality was poorer in 1989 compared to 1991. Although nitrogen content of washed rumen materials was higher in 1989, the greater abundance of graminoids and shrubs also increased the levels of ADF and lignin/cutin in the diet. Since lichens are low in nitrogen, and a good source of digestible energy (Thomas and Kroeger 1980), a reduced nitrogen content of washed rumen material may not be indicative of a poor winter diet. Nitrogen content of winter forage samples is not related to digestibility, rather, only carbohydrate content of forage correlates well with *in vitro* and nylon bag dry matter digestibility (Klein 1990).

Observed differences in winter diet as determined by the point estimate and microhistological techniques were likely a result of two related factors. Firstly, various plant species are digested at different rates in a rumen (Gaare *et al.* 1977, Thomas and Kroeger 1980). Secondly, plant material retained on the 2 mm screen represents recently ingested forage (Klein and Schonheyder 1970) and constitutes only a portion of total rumen contents. As particle size decreases, percentage of lichens invariably increases (Courtright 1959). Since I used the point estimate technique on plant material retained by the 2 mm screen, abundance of lichens was underestimated whereas graminoids and woody twigs were overestimated relative to the microhistological analysis of all rumen material. Results obtained by the microhistological analysis may be less affected by differential digestion and fragmentation of plant material and thus provide a more accurate assessment of proportionate intake (Thomas and Barry 1991).

Body condition

During the March 1989 survey, estimates of liveweights were unreliable because most weights were beyond the capacity of the scale (Arraguatinaq *et al.* 1990). Thus differences in liveweights of adult females between 1989 and 1990 reflect differences between scales rather than true differences in body weight.

Liveweights for adult female caribou and reindeer vary from approximately 55 to 118 kg (Reimers 1983a, Figure 1). These differences in body size are due to genetic and environmental factors. Genetic factors set the limit for growth rate and ultimate body size whereas environmental factors control growth rate and size attained (Reimers

1983a). Condition of summer range seems to be the main environmental determinant of body size in *Rangifer* but its interaction with winter range condition and harassment (insects and predators) is also important (Reimers 1983, but see Skogland 1983). Mean liveweights of adult female reindeer on the Belchers was 101.7 ± 2.3 kg. This places them in the upper range of body size for *Rangifer*. More importantly, adult females on the Belchers are comparatively large with respect to genetically related reindeer in the Mackenzie Delta and similar to domestic reindeer in Alaska (Table 3-8). Since liveweights of ruminants vary according to gut fill and show marked seasonal fluctuations direct comparisons are difficult. However, the seasonal nadir in liveweight of *Rangifer* occurs in late winter/early spring with peak weights occurring in late summer and early fall (Reimers and Ringberg 1983, Adamczewski *et al.* 1987b). As March weights of adult cows on the Belchers were substantially greater than liveweights of adult females in the Mackenzie Delta herd in July (Table 3-8), I argue that Belcher Island reindeer are larger than reindeer at the Reindeer Grazing Reserve. March weights of Belcher Island reindeer are similar to a) summer weights of reindeer prior to and during the recovery phase after the population crash of reindeer on St. Matthew Island (Klein 1968), and b) March weights of domestic reindeer at the University of Alaska (Cameron and Luick 1972) (Table 3-8). Belcher Island reindeer are also similar in liveweight to reindeer in Russia. In sum, although the data are sparse, these liveweight comparisons suggest that range conditions on the Belcher Islands are favorable and allow rapid growth in reindeer. Adult body size may be close to the genetic potential of this population. Large body size and rapid rates of individuals are expected when an ungulate population is introduced to a new environment where per capita food availability is high (Ouellet 1992).

Mass of the gastrocnemius and femur and depth of back fat are strongly related to carcass muscle, carcass bone, and carcass dissectible fat respectively (Ringberg *et al.* 1981, Reimers and Ringberg 1983, Adamczewski *et al.* 1987a). Since there were no significant differences in indicator tissues among years, body condition of reindeer and hence body reserves were likely similar over the three winters (1989-91). Thus, I argue that Belcher Island reindeer were not limited by winter forage as fat reserves were not depleted. This implies that forage was readily accessible during the winter months prior to the collection period. A crude comparison of back fat between Belcher Island reindeer and caribou on Coats and Southampton Island supports this argument. Average depth of back fat for adult female reindeer on the Belcher Islands collected in March from 1989-91 was 26 ± 3 mm (n = 13). Adamczweski *et al.* (1993) showed that during winter 1982-83, female caribou relied less on body reserves to satisfy

energetic requirements. Subsequently, depth of back fat for Coats Island caribou in winter 1982-83 declined from 53 mm in early November, to 33 and 10 mm in late March and late May respectively. In winter 1983-84, Coats Island caribou depleted body reserves much quicker, and depth of back fat declined at a rapid rate. Mean values of back fat measured in late October, March, and May were 50, 4, and 1 mm respectively. On Southampton Island where winter forage was comparatively abundant, Ouellet (1992) found that caribou maintained fat reserves during winter and rather relied more on protein reserves (carcass muscle) to meet energy requirements. Mean depth of back fat for adult female caribou on Southampton Island collected in May from 1988-91 was 22 $\pm$ 1 mm (n = 70, Ouellet unpublished data).

Despite localized overgrazing of lichen-dominated range on the Belcher Islands (Chapter 2), lichens are a principal component of late winter diets. Reindeer have been able to select a nutritionally adequate diet and satisfy their winter energetic requirements from forage. This is reflected by their relatively large body size and undepleted body reserves in late winter. Thus, I conclude that winter range presently is not a limiting factor in the ecology of this introduced population. However, future monitoring of both body condition and diet selection of Belcher Island reindeer is essential as the population reaches "carrying capacity." Range and snow conditions should be monitored regularly and concurrently so that their effects may be correlated to condition of reindeer. Correlative evidence does not reveal causal factors but it can be used to reject possible explanations.

Table 3-1. Average number of reindeer pellet-groups (± standard deviation) counted within belt transects (2m x 100m) on the Belcher Islands. Sample sizes are presented in parentheses.

Camp† Location	Range Communities†† 1 Barren bedrock ridges	2 Lichen dwarf shrub gravel ridges	3 Mixed lichen-dwarf shrub flats	4 Mixed lichen-dwarf shrub-sedge-moss hummocky meadows	5 Dwarf shrub-sedge-moss hummocky meadows	6 Sedge moss stream beds	Mean No. of Pellet-groups per Transect (Data pooled by camp location)
1	2 (1)	-	56 (1)	-	-	-	29.0 (2)
2	-	32.5 ± 10.6 (2)	38 (1)	7 (1)	-	5 (1)	23.0 (5) (5.5 - 50.1)†††
3	0 (1)	-	0 (1)	0 (1)	-	-	0 (3)
A	0 (8)	18.3 ± 15.7 (6)	21.0 ± 13.9 (7)	8.4 ± 9.5 (11)	5.5 ± 3.6 (6)	-	10.3 (38) (6.6 - 14.1)
B	0.7 ± 1.2 (3)	22.3 ± 15.7 (6)	63.7 ± 47.9 (3)	67 (1)	31.8 ± 30.5 (4)	69.0 ± 2.8 (2)	34.7 (19) (6.1 - 34.8)
C	7.7 ± 16.5 (6)	5.5 ± 2.0 (4)	14.3 ± 11.2 (6)	8.4 ± 9.5 (11)	5.3 ± 9.1 (6)	3.1 ± 5.1 (9)	7.3 (42) (4.2 - 10.4)
D	5.5 ± 4.9 (2)	35.5 ± 2.1 (2)	134.8 ± 43.2 (5)	26.7 ± 13.6 (6)	16.5 ± 3.5 (2)	23 (1)	54.0 (18) (15.4 - 65.2)
S	0 (1)	0 (1)	0 (4)	0 (4)	0 (4)	0 (3)	0 (17)

† See Figure 2.1 for locations of base camps.
†† Range communities are described in Chapter 2.
††† 95% Confidence intervals for negative binomial data (p. 92. Krebs 1989)

Table 3-2. Pairwise comparisons of observed pellet-group distributions from four base camps using Kolmogorov-Smirnov two sample tests.

	Camp			
Camp*	A	B	C	D
A	-			
B	0.019	-		
C	0.170	0.002	-	
D	<0.001	0.673	<0.001	-

*Camp locations shown on Figure 2-1.

Table 3-3. Composition of summer diet of Belcher Island reindeer. The micro-histological technique (Sparks and Malechek 1968) was used to estimate mean percent relative density (± SD) of plant cuticular fragments in fecal samples composited by year. Means based on four slides of 20 fields each.

Vegetation Class	July 1990	July-August 1991
Graminoids		
Carex spp.	-	0.9 (1.1)
Festuca spp.	-	0.4 (0.8)
Lichens		
Cladonia and *Cladina* spp.	0.4 (0.8)	1.5 (2.0)
Shrubs		
Salix spp.	99.2 (1.0)	97.2 (2.7)
Sheperdia spp.	0.4 (0.8)	-

Table 3-4. Composition of rumens collected from Belcher Island reindeer in late winter. The point estimate technique (Chamrad and Box 1964) was used to estimate mean proportion (±SE) of plant fragments retained on a 2 mm sieve for each rumen sample. The micro-histological technique (Sparks and Malechek 1968) was used to estimate mean percent relative density (± SD) of plant cuticular fragments in rumen samples composited by year. Means based on four slides of 20 fields each.

Vegetation Class	POINT ESTIMATE TECHNIQUE 1989 (n = 9)	1991 (n = 11)	$\bar{X}$
Graminoids (total)	48.7 (3.5)	38.7 (1.6)	43.7
living	0.4 (0.2)	0.9 (0.2)	
dead	48.3 (3.4)	37.9 (1.6)	
Shrubs (total)	28.5 (2.4)	26.0 (1.4)	27.3
leaves (living and dead)	9.7 (1.1)	10.5 (0.8)	
twigs	8.3 (1.2)	6.5 (0.5)	
Vaccinium spp. leaves*	8.0 (1.0)	5.3 (0.4)	
Vaccinium spp. twigs	2.5 (0.4)	3.7 (0.6)	
Lichens (total)*	10.4 (1.1)	21.6 (1.3)	16.0
Cetraria spp.*	3.6 (0.7)	6.3 (0.6)	
Cladina spp.*	5.6 (0.8)	12.1 (1.2)	
Other lichens*	1.2 (0.3)	3.2 (0.5)	
Mosses	8.9 (1.1)	11.2 (1.2)	10.1
Forbs†	1.3 (0.4)	0.5 (0.2)	0.9
Unknown	2.2 (0.2)	2.0 (0.1)	2.1

Vegetation Class	MICRO-HISTOLOGICAL TECHNIQUE 1989 (n = 1)	1991 (n = 1)	$\bar{X}$
Graminoids (total)	19.6	20.6	20.1
Carex spp.	18.5 (11.3)	19.9 (3.9)	
Eriophorum spp.	-	0.7 (1.4)	
Festuca spp.	1.1 (2.2)	-	
Shrubs (total)	20.5	6.4	13.5
Dryas integrifolia	7.1 (3.7)	2.5 (3.3)	
Empetrum nigrum	11.6 (2.7)	1.5 (1.7)	
Salix spp.	0.9 (1.8)	0.8 (1.5)	
Sheperdia canadensis	0.9 (1.9)	0.8 (1.5)	
Vaccinium spp.	-	0.8 (1.7)	
Lichens (total)	51.6	61.2	56.4
Alectoria spp.	-	1.6 (1.9)	
Cetraria spp.	1.1 (2.1)	4.9 (2.0)	
Cladina and *Cladonia* spp.	50.5 (12.1)	53.2 (9.0)	
Peltigera spp.	-	1.6 (1.9)	
Mosses	8.3 (8.8)	11.8 (4.4)	10.1

* $p \leq 0.01$

† Mostly *Pyrola grandiflora*

Table 3-5. Percentage of lichens and shrubs identified using the point estimate technique on rumen contents collected in late winter.

	March 1989	March 1991
Number of rumen samples	9	11
Lichens		
	(187)*	(474)
Alectoria ochroleuca	1	2
Bryocaulon divergens	1	3
Cetraria nivalis	28	26
Cetraria islandica	6	3
Cladina mitis	41	45
Cladina rangiferina	12	11
Cladonia spp.	2	4
Thamnolia vermicularis	-	t**
Foliose lichen	9	6
Total	100	100
Shrubs		
	(514)	(572)
Dryas integrifolia	5	6
Empetrum nigrum	2	2
Rhododendron lapponicum	2	1
Salix spp.	55	57
Vaccinium uliginosum	20	21
Vaccinium vitis-idaea	16	14
Total	100	100

* Total number of hits incurred during point sampling.
** trace (less than 1%)

Table 3-6. Nutritive quality (% ± SE) of washed rumen contents of reindeer collected on the Belcher Islands, Northwest Territories.

Nutritional parameter	March 1989 (n = 9)	March 1991 (n = 11)
NDF	64.1 (3.7)	64.5 (2.9)
ADF	36.3 (2.4)[a *]	32.2 (2.0)[b]
Lignin / cutin	16.0 (1.2)[a]	14.1 (1.0)[b]
Nitrogen	2.5 (0.3)[a]	2.1 (0.2)[b]

*Letters denote significant differences between years ($p \leq 0.001$)

Table 3-7. Liveweights and indices of body condition for Belcher Island reindeer in March (1989-1991). Means are presented with standard errors; sample sizes in brackets.

Measurement	1989	1990	1991	Mean
Adult Females				
Liveweight (kg)	95.8 ± 2.4 (5)[a*]	109.0 ± 4.3 (6)[b]	98.8 ± 2.4 (5)[ab]	101.7 ± 2.3
Gastrocnemius[†] (g)	436 ± 13 (5)	475 ± 25 (4)	405 ± 16 (4)	438 ± 12
Femur (g)	436 ± 7 (5)	425 ± 25 (4)	406 ± 12 (4)	423 ± 9
Femur (mm)	267 ± 3 (5)	271 ± 7 (4)	268 ± 4 (4)	268 ± 3
DBF[††] (mm)	24 ± 5 (4)	30 ± 7 (4)	25 ± 5 (5)	26 ± 3
Subadult Females				
Live weight (kg)	79.5 ± 4.5 (2)	77 (1)	89.5 ± 3.5 (2)	83.0 ± 3.2
Gastrocnemius (g)	400 ± 0 (2)	350 (1)	405 ± 16 (2)	392 ± 12
Femur (g)	410 ± 5 (2)	350 (1)	438 ± 13 (2)	409 ± 23
Femur (mm)	256 ± 11 (2)	248 (1)	278 ± 6 (2)	263 ± 7
DBF (mm)	26 ± 4 (2)	8 (1)	28 ± 3 (2)	23 ± 4
Subadult Males				
Live weight (kg)	79.7 ± 5.2 (3)	79.3 ± 2.6 (3)	92.3 ± 3.5 (3)	83.8 ± 2.9
Gastrocnemius (g)	423 ± 12 (3)	483 ± 44 (3)	399 ± 43 (3)	435 ± 22
Femur (g)	403 ± 26 (3)	417 ± 44 (3)	475 ± 25 (3)	432 ± 20
Femur (mm)	261 ± 9 (3)	267 ± 10 (3)	281 ± 3 (3)	270 ± 4
DBF (mm)	-	19 ± 16 (2)	7 ± 2 (3)	12 ± 6

[†] In March 1991, weights of gastrocnemius muscles included the flexor digitalis and were adjusted accordingly (Adamczewski *et al.* 1988)

[††]Depth of back fat

[*] Means in the same row with different superscript letters are significantly different at $p < 0.05$.

Table 3-8. Average weight of adult female reindeer on the Belcher Islands and comparative data from other reindeer herds in North America and Russia.

Herd	liveweight (kg)	Reference
Belcher Islands (19)† (March 1989-1991)	101.7 (90-122)††	This study and Arragutainaq *et al.* 1990
Mackenzie Delta (15) (July 1958)	85.7 (69-95)	Krebs and Cowan 1962
Alaska		
St. Matthew Island		Klein 1968
(July-Aug 1957) (12)	111.6 (111.1-112.0)	
(July 1963) (15)	77.6 (68.0-87.5)	
(July 1966) (10)	94.3 (86.2-100.7)	
Univ. of Alaska (5) Reindeer Research Station (March 1970)	97.7 (79.0-112.0)	Cameron and Luick 1972
Russia		Skjenneberg and Slagsvold 1968
Murmansk District (131)	103.5	
Kolgujev Island (64)	117.6	
Malosemeljskaja tundra (1061)	95.3	
West Ural (77)	102.6	
Jamal (112)	98.5	
Taimyr National Territory (40)	68.0	
Tofalaria (105)	111.4	
Russsia	87 - 105	Staaland and Nieminen 1993
Wild	86 -116	
Evenki reindeer	110 -120	

† Sample size
†† Range

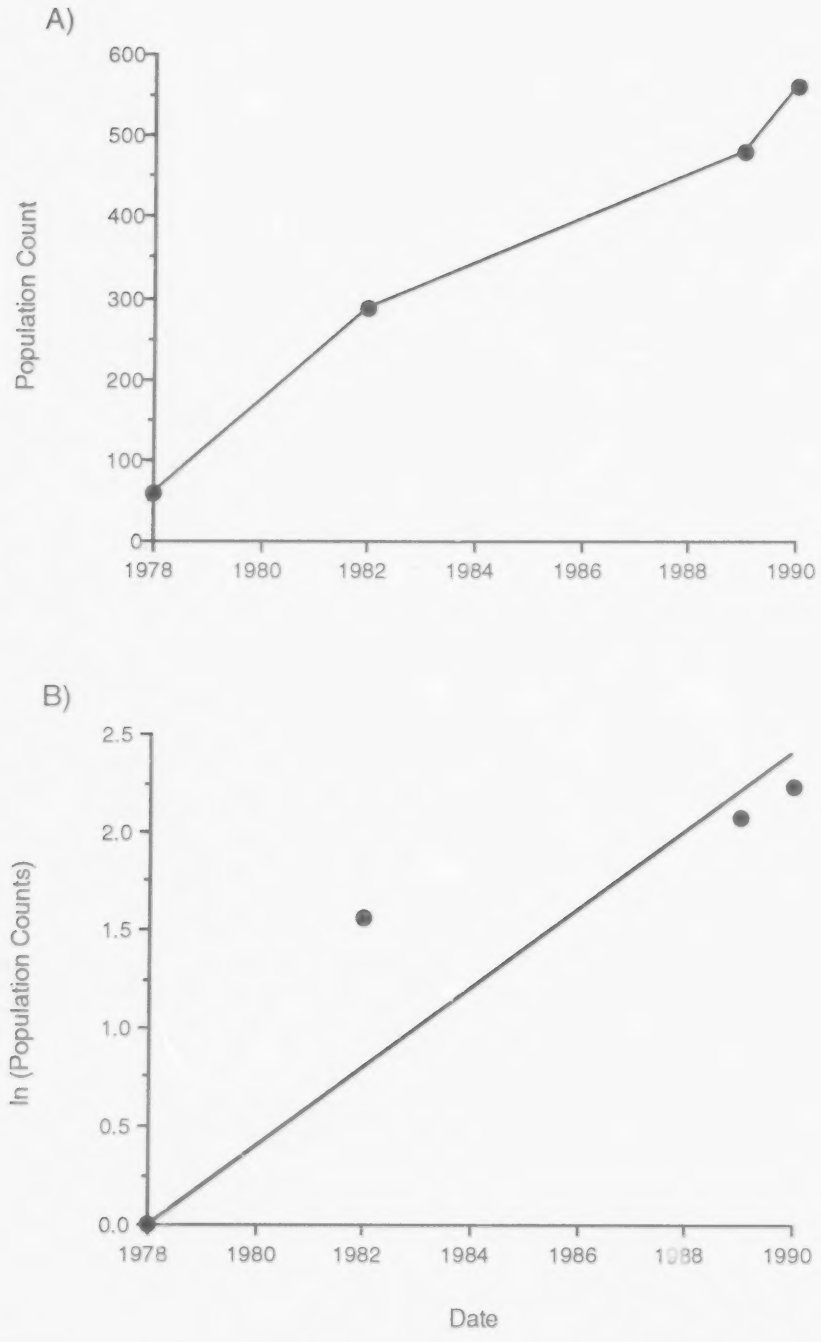


Figure 3-1. A) Population counts of reindeer introduced to the Belcher Islands, Northwest Territories, 1978 - 90 (data from Ferguson (1985) and Arragutainaq *et al.* (1990)). The original herd was introduced in March 1978 and consisted of 50 adult females and 10 adult males. B) Observed rate of increase of reindeer; the curve was constrained to pass through the number of animals introduced in 1978 ($y = 4.09 + 0.20\ x$, $r^2 = 0.95$, $p = 0.005$; where x is years since introduction).

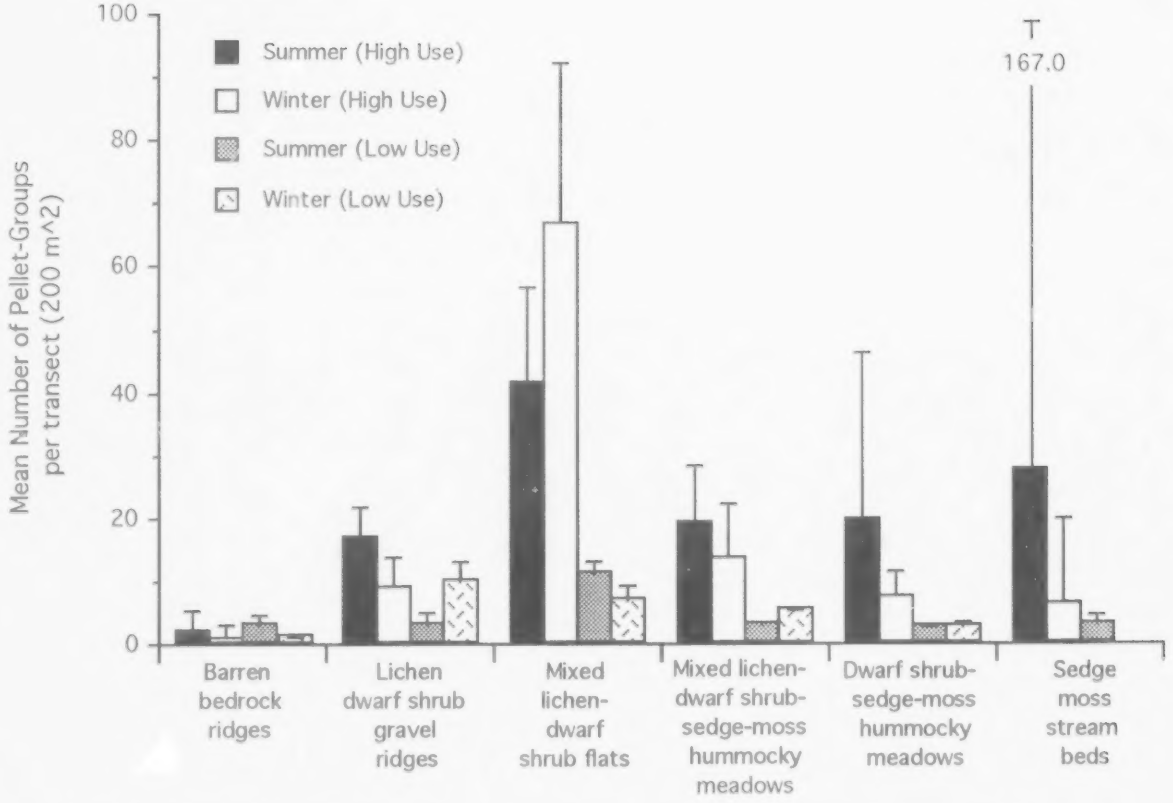


Figure 3-2. Average densities of reindeer pellet-groups in different range communities on the Belcher Islands. Bars represent the upper 95% confidence limit of the mean. In the legend, "Summer" and "Winter" refer to the classification of pellet-groups; summer type pellets were an amorphous mass of several individual pellets whereas winter pellets were hard and spherical. Data from Camps A and C, and Camps B and D were pooled into "Low Use" and "High Use" groups respectively (see Analyses).

Literature Cited

Adamczewski, J.Z., C.C. Gates, and R.J. Hudson. 1987a. Fat distribution and indices of carcass composition in Coats Island caribou *(Rangifer tarandus groenlandicus)*. Canadian Journal of Zoology. 65: 368-374.

Adamczewski, J.Z., C.C. Gates, R.J. Hudson, and M.A. Price. 1987b. Seasonal changes in body composition of mature female caribou and calves *(Rangifer tarandus groenlandicus)* on an arctic island with limited winter resources. Canadian Journal of Zoology. 65: 1149-1157.

Adamczewski, J.Z., C.C. Gates, B.M. Soutar, and R.J. Hudson. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou *(Rangifer tarandus groenlandicus)* on Coats Island, Northwest Territories, Canada. Canadian Journal of Zoology. 66: 1986-1996.

Adamczewski, J.Z., R.J. Hudson, and C.C. Gates. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. Canadian Journal of Zoology. 71: 1221-1229.

Arragutainaq, L., R.J. Hudson, and P. Poole. 1990. Reindeer surveys on the Belcher Islands. 1989-1990. Weasels Hunters and Trappers Association. Sanikiluaq, Northwest Territories. X0A-0W0. unpublished report. 19 pp.

Baskin, L.M. 1989. Reindeer husbandry in the Soviet Union. Chapter 10. In: Hudson, R.J., K.R. Drew, and L.M. Baskin, editors. Wildlife Production Systems: Economic Utilization of Wild Ungulates. Cambridge University Press, Cambridge, England.

Bergerud, A.T. and L. Russell. 1964. Evaluation of rumen food anlaysis for Newfoundland caribou. Journal of Wildlife Management. 28: 809-814.

Boertje, R.D. 1984. Seasonal diets of the Denali caribou herd, Alaska. Arctic. 37: 161-165.

Boertje, R.D., J.L. Davis, and P. Valkenburg. 1985. Uses and limitations of fecal analyses in *Rangifer* studies. pages 307-316. In T.C. Meredith and A.M. Martell (eds). Proceedings of the 2nd North American Caribou Workshop. Val Morin, Quebec.

Bowden, D.C., A.E. Anderson, and D.E. Medin. 1969. Frequency distributions of mule deer fecal group counts. Journal of Wildlife Management. 33: 895-905.

Cameron, R.D., and J.R. Luick. 1972. Seasonal changes in total body water, extracellular fluid, and blood volume in grazing reindeer. Canadian Journal of Zoology. 34: 48-52.

Caughley, G. 1977. Analysis of Vertebrate Populations. John Wiley and Sons, New York, New York, USA.

Chamrad, A.D., and T.W. Box. 1964. A point frame for sampling rumen contents. Journal of Wildlife Management. 28: 473-477.

Collins, W.B., and P.J. Urness. 1981. Habitat preferences of mule deer as related by pellet-group distributions. Journal of Wildlife Management. 45: 969-972.

Collins, W.B. and T.S. Smith. 1991. Effects of wind-hardened snow on foraging by reindeer *(Rangifer tarandus)*. Arctic. 44: 217-222.

Courtright, A.M. 1959. Range management and the genus *Rangifer*. A review of selected literature. M.Sc. thesis. University of Alaska. 172 pp.

Crete, M., J. Huot, and L. Gauthier. 1990. Food selection during early lactation by caribou calving on the tundra in Quebec. Arctic. 43: 60-65.

Dauphine, T.C. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. Canadian Wildlife Service Report Series Number 38. 71 pp.

Dearden, B.L., R.E. Pegau, and R.M. Hansen. 1975. Precision of microhistological estimates of ruminant food habits. Journal of Wildlife Management. 39: 402-407.

Edmonds, E.J. 1979. A study of reindeer *(Rangifer tarandus tarandus)* range on the Belcher Islands, Northwest Territories. Unpublished report. Canadian Wildlife Service. 37 pp.

Elliot, J.M. 1977. *Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates*. 2nd Edition. Freshwater Biological Association Scientific Publication No. 25. 160 pp.

Ferguson, M.A.D. 1985. Population status of introduced reindeer on the Belcher Islands, Northwest Territories, in March 1982. Northwest Territories Wildlife Service File Report No. 45. 18 pp.

Fuller, T. 1991. Do pellet counts index white-tailed deer numbers and population change? Journal of Wildlife Management. 55: 393-396.

Gaare, E., A. Sorensen, and R.G. White. 1977. Are rumen samples representative of the diet? Oikos. 29: 390-395.

Gates, C.C., Adamczewski, J., and R. Mulders. 1986. Population dynamics, winter ecology, and social organization of Coats Island caribou. Arctic. 39: 216-222.

Godkin, G.F. 1986a. Fertility and twinning in Canadian reindeer. Rangifer Special Issue No. 1: 145-150.

Godkin, G.F. 1986b. The reindeer industry in Canada. Canadian Veterinary Journal. 27: 488-490.

Goering, H.K., and P.J. Van Soest. 1970. Forage fiber analysis. Agriculture Handbook No. 379. Agriculture Research Service, U.S. Department of Agriculture.

Heard. D. 1990. The intrinsic rate of increase of reindeer and caribou populations in arctic environments. Rangifer. 3: 169-173.

Holechek, J.L., M. Vavra, and R.D. Pieper. 1982. Botanical composition determination of range herbivore diets: a review. Journal of Range Management. 35: 309-315.

Jefferies, R.L., J. Svoboda, G. Henry, M. Raillard, and R. Ruess. 1992. Tundra grazing systems and climatic change. In. Arctic Ecosystems in a Changing Climate. Academic Press, New York, New York, USA.

Klein, D.R. 1962. Rumen contents analysis as an index to range quality. Transactions of the North American Wildlife and Natural Resources Conference. 27: 150-164.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management. 32: 350-367.

Klein, D.R. 1986. Latitudinal variation in foraging strategies. pages 237-246. In O. Gudmundsson, editor. Grazing Research at Northern Latitudes. NATO Advanced Research Workshop. Hvanneyri, Iceland.

Klein, D.R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant parts, and phenology. Rangifer Special Issue No. 3: 123-130.

Klein, D.R., and F. Schonheyder. 1970. Variation in ruminal nitrogen levels among some cervidae. Canadian Journal of Zoology. 48: 1437-1442.

Krebs, C.J. 1989. Ecological Methodology. Harper and Row, New York, New York, USA.

Laperriere, A.J., and P.C. Lent. 1977. Caribou feeding sites in relation to snow characteristics in northeastern Alaska. Arctic. 30: 101-108.

Leader-Williams, N. 1988. Reindeer on South Georgia: The Ecology of an Introduced Population. Cambridge University Press, Cambridge, England.

McConnell, B.R. and J.G. Smith. 1970. Frequency distribution of deer and elk pellet groups. Journal of Wildlife Management. 34: 29-36.

Miller, F.L. 1974. Eruption and attrition of mandibular teeth in barren-ground caribou. Journal of Wildlife Management. 36: 606-612.

Miller, F.L., R.R. Russell, and A. Gunn. 1977. Interisland movements of Peary caribou *(Rangifer tarandus pearyi)* on western Queen Elizabeth Islands, Arctic Canada. Canadian Journal of Zoology. 55: 1029-1037.

Neff, D.J. 1968. The pellet-group count technique for big game trend, cencus, and distribution: a review. Journal of Wildlife Management. 32: 597-614.

Ouellet, J.P. 1992. Ecology on an introduced caribou population on Southampton Island, N.W.T., Canada. Ph.D. Thesis. University of Alberta. Edmonton, Alberta. 123 pp.

Parker, G.R. 1978. The diets of muskoxen and peary caribou on some islands in the Canadian High Arctic. Canadian Wildlife Service Occasional Paper No. 35. 19 pp.

Parker, G.R. 1981. Physical and reproductive characteristics of an expanding woodland caribou population *(Rangifer tarandus caribou)* in northern Labrador. Canadian Journal of Zoology. 59: 1929-1940.

Popko, R. 1979. Reindeer - Aerial Survey, Belcher Islands, N.W.T., July 1979. Unpubl. letter to A. Bourque, Regional Superintendent, N.W.T. Wildlife Service, Frobisher Bay, N.W.T. 7pp.

Pruitt, W.O. 1959. Snow as a factor in the winter ecology of the barren ground caribou. Arctic. 12: 158-179.

Reimers, E. 1972. Growth in domestic and wild reindeer in Norway. Journal of Wildlife Management. 36: 612-619.

Reimers, E. 1983a. Growth rate and body size differences in *Rangifer*, a study of causes and effects. Rangifer. 3: 3-15.

Reimers, E. 1983b. Reproduction in wild reindeer in Norway. Canadian Journal of Zoology. 61: 211-217.

Reimers, E., and T. Ringberg. 1983. Seasonal changes in body weights of Svalbard reindeer from birth to maturity. Acta Zoologica Fennica. 175: 69-72.

Ringberg, T., R.G. White, D.E. Holleman, and J.R. Luick. 1981. Prediction of carcass composition in reindeer *(Rangifer tarandus tarandus* L.) by use of selected indicator bones and muscles. Canadian Journal of Zoology. 59: 583-588.

Rowland, M.M., G.C. White and E.M. Karlen. 1984. Use of pellet-group plots to measure trends in deer and elk populations. Wildlife Society Bulletin. 12: 147-155.

Scheffer, V.B. 1951. The rise and fall of a reindeer herd. Scientific Monthly. 73: 356-362.

Scotter, G.W. 1966. Sieve mesh size as related to volumetric and gravimetric analysis of caribou rumen contents. Canadian Field-Naturalist. 80: 238-241.

Scotter, G.W. 1972. Reindeer ranching in Canada. Journal of Range Management. 25: 167-174.

Scotter, G.W. 1978. How Andy Bahr led the great reindeer herd from western Alaska to the Mackenzie Delta. Canadian Geography Journal. 97: 12-19.

Skjenneberg, S., and L. Slagsvold. 1968. Reindeer husbandry and its ecological principles. Translated from Norwegian by C.M. Anderson and J.R. Luick. 1979. U.S. Department of the Interior, Bureau of Indian Affairs. Juneau, Alaska, USA.

Skogland, T. 1978. Characteristics of the snow cover and its relationship to wild mountain reindeer *(Rangifer tarandus tarandus* L.) feeding strategies. Arctic and Alpine Research. 10: 569-580.

Skogland, T. 1983. The effects of density dependant resource limitation on size of wild reindeer. Oecologia. 60: 156-168.

Skogland, T. 1984. Wild reindeer foraging-niche organization. Holarctic Ecology. 7: 345-379.

Skogland, T. 1985. The effects of density-dependant resource limitation on the demography of wild reindeer. Journal of Animal Ecology. 54: 359-374.

Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd. Oecologia. 84: 442-450.

Sokal, R.R. and F.J. Rohlf. 1980. Biometry: The Principles and Practices of Statistics in Biological Research. W.H. Freeman and Company. San Fransico, California, USA.

Sparks, D.R., and J.C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management. 21: 264-265.

Staaland, H., and M. Nieminen. 1993. World reindeer herding: origin, history, distribution, economy. pages 161-203. In Proceedings of the VII World Conference on Animal Production. Edmonton, Alberta, Canada.

Staaland, H., J.O. Scheie, F.A. Grøndahl, E. Persen, A.B. Leifseth, and Ø. Holand. 1993. The introduction of reindeer to Brøggerhalvøya, Svalbard: grazing preference and effect on vegetation. Rangifer. 13: 15-19.

Stormer, F.A., T.W. Hoekstra, C.M. White, and C.M. Kirkpatrick. 1977. Frequency distribution of deer pellet groups in southern Indianna. Journal of Wildlife Management. 41: 779-782.

Thomas, D.C. 1982. The relationship between fertility and fat reserves of Peary caribou. Canadian Journal of Zoology. 60: 597-602.

Thomas, D.C. and Kroeger. 1980. *In vitro* digestibilities of plants in rumen fluids of Peary caribou. Arctic. 33: 757-767.

Thomas, D.C. and D.P. Hervieux. 1986. The late winter diets of barren-ground caribou in North-Central Canada. Rangifer Special Issue No. 1: 305-310.

Thomas, D.C., and S.J. Barry. 1991. Microhistological analyses of caribou diet: fecal versus rumen and other variables. pages 516-529. In C.E. Butler and S.P. Mahoney (eds). Proceedings of the 4th North American Caribou Workshop. St. John's Newfoundland, Canada.

Thompson, D.C. and K.H. McCourt. 1981. Seasonal diets of the Porcupine caribou herd. American Midland Naturalist. 105: 70-76.

Tyler, N.J.C. 1987. Natural limitation of the abundance of the High Arctic Svalbard reindeer. Ph.D. Thesis. University of Cambridge. Cambridge, England. 327 pp.

Tyler, N.J.C., and N.A. Øritsland. 1989. Why don't Svalbard reindeer migrate? Holarctic Ecology. 12: 369-376.

Vavra, M., and J.L. Holechek. 1980. Factors influencing microhistological analysis of herbivore diets. Journal of Range Management. 33: 371-374.

White, G.C. and L.E. Eberhardt. 1980. Statistical analysis of deer and elk pellet-group data. Journal of Wildlife Management. 44: 121-131.

Wilkinson, L., M. Hill, S. Miceli, P. Howe, and E. Vang. 1992. SYSTAT: Version 5.2 Edition. Systat Inc., Evanston, Illinois, USA.

Chapter 4

General Discussion

This study provided an opportunity to document the interaction between a recently introduced population of reindeer and the vegetation on which it forages. My specific objectives were: a) to determine whether grazing by reindeer had reduced available forage (Chapter 2), and b) to determine whether reduced forage availability may have affected seasonal range use and diet, or body condition of reindeer in late winter (Chapter 3).

My principal conclusion in Chapter 2 was that Belcher Island reindeer have overgrazed lichen-dominated range communities in heavily used areas of southwest Flaherty Island. In those overgrazed range communities there was a near total depletion of usable lichens. Abundance of grasses and forbs was significantly lower whereas cover of evergreen dwarf shrubs, litter, and bare ground was greater at heavily grazed sites than ungrazed sites. Because lichens may require at least 20 - 30 years to regrow in the absence of continued grazing (see Klein 1987), it is clear that reindeer have overgrazed those areas of lichen range. Nevertheless, lichens still represent greater than 50% of the rumen contents of reindeer in late winter (Chapter 3).

Another important finding was that intense browsing of willows by reindeer in summer has likely hastened mortality of those plants. Shoots of willows in heavily grazed areas had significantly greater proportion of attached dead material and significantly less current growth and live woody material than unbrowsed willows (Chapter 2). In addition to these differences in patterns of aboveground biomass allocation, current growth of willows at heavily browsed sites had significantly greater concentrations of nitrogen and phosphorous than willows at unbrowsed sites. Increases in N and P content suggest a compensatory response to browsing. These findings are important because willows are a plant species generally known for their rapid rates of growth and their ability to recover from brief episodes of intense browsing (Henry and Gunn 1991). Thus, browsing must have been intensive and sustained throughout the growing season and over consecutive summers to account for those observed differences in growth habit and nutrient concentration. These findings comply with the hypothesis that abundance of deciduous shrubs (*i.e.*, digestible protein) during summer may be an important regulating factor in the ecology of *Rangifer* (Crete *et al.* 1990).

In Chapter 3, my assessment of seasonal use of range and forage plants by reindeer confirmed the importance of lichens and willows in winter and summer respectively. Those results provided strong circumstantial evidence that reindeer were the cause of poor range condition of lichen and willow-dominated vegetation communities in southwest Flaherty Island. Despite localized overgrazing, Belcher Island reindeer are comparatively large with respect to genetically related reindeer in North America. Large body size and rapid growth rates of individuals are expected when an ungulate population is introduced to a new environment where per capita food availability is high (Ouellet 1992). Reindeer were in good body condition during late winter; adult females still had excess fat reserves in late winter suggesting that food availability was not limiting. These results show that there is a lag between the time that lichens are overgrazed and the time that reindeer become negatively affected.

Management Implications

The objective of managing reindeer on the Belcher Islands is to provide a sustainable source of meat for local residents while ensuring persistence and stability of the reindeer population. However, there is much that we do not know about the factors that determine trends in population numbers of *Rangifer* through time (see Caughley and Gunn 1993). To estimate carrying capacity (K) (see Macnab 1989) in a fluctuating environment is often a futile and dangerous exercise because it (K) implies that a system can sustain a constant or relatively stabile number of animals (see Wiens 1977). Thus, a harvest scheme based on the notion of a set carrying capacity is inflexible and increases the probability of overharvesting a population especially when numbers of animals may vary widely as in arctic environments.

In this study, I found that introduced reindeer on the Belcher Islands are still increasing and in good body condition during late winter despite localized overgrazing of lichen and willow-dominated range communities in heavily used areas. This implies that this population is still in the early stages of Riney's (1964) conceptual model of the dynamics of an irruptive oscillation. That is, introduced reindeer are increasing in numbers despite a decline in the trend of vegetation in critical areas. Thus, the most immediate threat to the long term persistence of reindeer on the Belcher Islands is uncontrolled irruptive population growth. In the past, reindeer introduced to island systems have increased rapidly and overgrazed lichen dominated range (Scheffer 1951, Klein 1968, and see Swanson and Barker 1992). As a result of their dependence on lichens as the main source of winter forage, overgrazing predisposed those populations to starvation in winter (Scheffer 1951, Klein 1968). Because of the slow growth rates

of lichens (see Sveinbjörnsson 1990), overgrazing can result in a time lag in the relationship between reindeer numbers and available food. Caughley and Lawton (1981) argue that stability in herbivore numbers is related to the temporal relationship between food availability and food limitation. Thus it follows that lichen-caribou/reindeer interactions and range expansion may both serve to increase instability in population numbers because they increase the time lag between food limitation and availability (Messier *et al.* 1988).

Hunting can be used to slow the rate of increase of an expanding population such that the adjustment between available forage resources and food requirements of the animals is made smoother (Messier *et al.* 1988). Hunting is therefore an important tool for managing an increasing population. Reindeer on the Belcher Islands are presently hunted at a recommended rate of 50% of the estimated number of yearlings (Ferguson 1985). This hunting scheme may be affecting the population via a reduction in the rate of increase (Chapter 3). Clearly, annual harvest levels should be compiled to determine whether this may be a possibility.

Recommendations

The Belcher Islands represent a unique management situation because reindeer are not considered indigenous wildlife (Anonymous 1982) and actually belong to the community, *i.e.,* the user is the manager. Thus, the onus to collect information to base management decisions is placed on the shoulders of the local Hamlet Council and Hunters and Trappers' Association. As a result, documentation of the traditional knowledge of local residents is of critical importance for management (Fleming 1991). In addition, I think that systematic collection of the following baseline information on a long-term basis is essential for continued management of this introduced reindeer population.

1) Population counts should be conducted at least every 5 years to determine trend in numbers. The snowmobile ground survey technique as described by Arragutainaq *et al.* (1990) should be continued as it relies on knowledge and expertise of local hunters. This technique seems to be relatively accurate (compared to aerial photographic surveys) and repeatable (Arragutainaq *et al.* 1990).

2) Numbers of animals killed by hunters should be recorded on an annual or even a monthly basis. Information from hunters regarding age, sex, and location of kill should also be recorded. Harvest levels should be reviewed in light of population counts, and other indicators of animal and range condition.

3) Hunters' observations of reindeer regarding seasonal range use and body condition should be compiled and documented. Body condition surveys should be continued in

conjunction with late winter hunts. Data collection should be restricted to a few indices of condition such as liveweight, depth of back fat, weight / length of femur, and weight of gastrocnemius muscle.

4) Weather conditions, *i.e.*, snow conditions, should be monitored (see Appendix 2). Weather observations could be collected in conjunction with environmental data recorded at the Sanikiluaq airport.

Literature Cited

Anonymous. 1982. In the Quebec superior provincial court, district of Montreal Gratton in Montreal: The Province of Quebec vs. G.Hudon. Court transcript of judgment, 25 June 1982. No. 500-36-044-8911. 7pp.

Arragutainaq, L., R.J. Hudson, and P. Poole. 1990. Reindeer surveys on the Belcher Islands. 1989-1990. Weasels Hunters and Trappers Association. Sanikiluaq, Northwest Territories. X0A-0W0. unpublished report. 19 pp.

Caughley, G. and A. Gunne. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. Oikos. 67: 47-55.

Caughley, G., and J.H. Lawton. 1981. Plant-herbivore systems. pages 132-166. In: R.M. May, editor. Theoretical Ecology. Sinauer, Sunderland, Massachusetts, USA.

Crete, M., J. Huot, and L. Gauthier. 1990. Food selection during early lactation by caribou calving on the tundra in Quebec. Arctic. 43: 60-65.

Ferguson, M.A.D. 1985. Population status of introduced reindeer on the Belcher Islands, Northwest Territories, in March 1982. Northwest Territories Wildlife Service File Report No. 45. 18 pp.

Fleming, M.M. 1990. Documentation of traditional knowledge for adaptive management of a reindeer population in the Belcher Islands, Canada. Belcher Island Adaptive Reindeer Management Project. Unpublished report. 16 pp. Sanikiluaq, N.W.T. X0A-0W0.

Henry, G.H.R., and A. Gunn. 1991. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic. 44: 38-42.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management. 32: 350-367.

Klein, D.R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. Journal of Range Management. 40: 336-338

Macnab, J. 1985. Carrying capacity and related slippery shibboleths. Wildlife Society Bulletin. 13: 403-410.

Messier, F., J. Huot, D. Le Henaff, and S. Luttich. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic. 41: 279-287.

Ouellet, J.P. 1992. Ecology on an introduced caribou population on Southampton Island, N.W.T., Canada. Ph.D. Thesis. University of Alberta. Edmonton, Alberta. 123 pp.

Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. IUCN Publications New Series No. 4: 261-273.

Scheffer, V.B. 1951. The rise and fall of a reindeer herd. Scientific Monthly. 73: 356-362.

Sveinbjörnsson, B. 1990. Reindeer lichen productivity: problems and possibilites. Rangifer Special Issue No. 3: 91-98.

Swanson, J.D., and M.H.W. Barker. 1992. Assessment of Alaska reindeer populations and range conditions. Rangifer. 12: 33-43.

Wiens, J.A. 1977. On competition and variable environments. American Scientist. 65: 590-597.

Appendix 1. Climatic data, based on records from meterological stations at Inukjuak (1921-1990) and Kuujjuarapik (1925-1990), Quebec. Data provided by Atmospheric Environment Service, Ville St-Laurent, Quebec.

Inukjuak (58°27' N; 78°07' O/W, 2m)

	Air Temperature (°C)					Precipitation (mm)			Degree-Days
	Mean	Mean of daily		Absolute extreme					
	daily	high	low	high	low	rain	snow	total	(> 5°C)
Month									
Jan.	-24.4	-20.6	-28.3	0.5	-46.1	0.01	13.0	12.6	0.0
Feb.	-25.5	-21.5	-29.7	5.0	-49.4	0.01	10.2	10.1	0.0
Mar.	-21.1	-16.3	-26.0	3.9	-45.0	0.1	12.7	12.4	0.0
Apr.	-11.2	-6.7	-15.9	7.2	-34.4	2.9	16.6	19.2	0.0
May	-1.9	1.2	-5.1	23.3	-25.5	9.8	13.7	23.2	1.8
June	4.2	7.9	0.4	30.0	-9.4	31.9	4.3	36.1	38.3
July	9.1	13.1	5.1	27.8	-6.7	54.7	0.7	55.1	132.6
Aug	8.9	12.1	5.7	25.6	-2.8	62.3	0.1	62.4	121.4
Sep.	5.1	7.8	2.4	22.8	-11.1	58.1	6.4	64.6	36.8
Oct.	-0.1	2.2	-2.4	15.7	-22.8	27.8	26.5	52.4	1.8
Nov.	-7.1	-3.9	-10.4	8.3	-33.9	3.0	44.9	44.9	0.0
Dec.	-18.1	-14.4	-22.1	16.3	-43.4	0.4	26.6	25.2	0.0
Year	-6.8	-3.3	-10.5	-	-	251.1	175.4	418.1	333

Appendix 1. continued

Kuujjuarapik (55°17' N; 77°46' O/W, 21m)

Month	Air Temperature (°C)					Precipitation (mm)			Degree-Days (> 5°C)
	Mean daily	Mean of daily high	Mean of daily low	Absolute extreme high	Absolute extreme low	rain	snow	total	
Jan.	-22.8	-8.3	-27.5	3.3	-49.4	0.01	30.0	28.1	0.0
Feb.	-23.1	-17.7	-28.7	13.8	-48.9	0.4	21.9	21.1	0.0
Mar.	-17.5	-11.5	-23.7	11.1	-45.0	1.5	21.1	21.1	0.0
Apr.	-7.1	-1.8	-12.6	21.9	-33.9	6.7	19.0	25.1	2.4
May	1.2	5.7	-3.4	28.3	-25.0	21.4	15.4	36.4	27.4
June	6.3	11.2	1.2	50.6	-7.8	50.6	6.3	57.3	86.6
July	10.2	15.1	5.2	33.3	-2.2	72.4	0.3	72.7	165.5
Aug.	10.6	14.9	6.3	33.3	-1.1	89.0	0.0	89.0	174.9
Sep.	7.2	10.7	3.7	33.9	-6.1	90.7	2.5	93.6	83.6
Oct.	2.1	4.9	-0.7	23.9	-15.0	44.3	29.7	73.7	14.5
Nov.	-5.0	-2.2	-7.9	11.5	-28.9	9.2	55.1	62.1	0.5
Dec.	-16.6	-12.6	-20.7	7.2	-46.1	0.7	37.0	35.1	0.0
Year	-4.5	-0.1	-9.1	-	-	387.1	238.2	614.9	556

Appendix 2

Snow surveys on the Belcher Islands

Introduction

Snow is one of the most important environmental factors that affects reindeer and caribou in winter (Pruitt 1959, 1979, Laperierre and Lent 1977, Skogland 1978, Adamczewski *et al.* 1988, Brown and Theberge 1990, Collins and Smith 1991). Snow may limit access to forage thereby reducing forage intake in grazing ungulates. An excessively deep or hard snowpack can make forage unavailable altogether. Characteristics of a snowpack are quantified primarily by measuring depth and hardness of each layer seperately and/or all the layers together. Snow pits have been commonly used to study snow profiles where total numbers of layers, and depth and hardness (measured with a spring penetrometer) of each layer are recorded (Pruitt 1959, 1979, Adamcweski *et al.* 1988, Brown and Theberge 1990). Alternatively, hardness of the snowpack can be measured with a Ramsonde penetrometer (Laperierre and Lent 1977, Skogland 1978, Brown and Theberge 1990, Collins and Smith 1991, Ouellet 1992). Wind hardened snow *(upsik)* (see Pruitt 1979) is more easily measured with a ramsonde penetrometer as opposed to conducting snow pit studies. Also, the Ramsonde provides a relatively quick and useful index of snow that gives a clear measure of the thresholds exibited by caribou and reindeer to snow hardness (Brown and Theberge 1990, Collins and Smith 1991).

On the Belcher Islands, introduced reindeer are increasing in number and are in excellent body condition in late winter (Chapter 3). This indicates that winter food availability, as affected by either range or snow conditions, has not limited food intake of reindeer. Lichen range has already been overgrazed in areas used heavily by reindeer (Chapter 2), and presumably extent of overgrazing will increase through time as the population increases. Therefore, it is important to collect long term data on winter snow conditions in order to differentiate between the potentially confounding effects of range and snow conditions on food availability and hence body condition of reindeer. My main objective was to determine variabilty in snow depth and hardness at a site using a Ramsonde penetrometer and to prescribe sampling methodology for future sampling on the Belcher Islands. My second objective was to determine whether snow depth and hardness was different between distinct range communities.

Methods and Materials

I conducted this snow survey on the northern part of Flaherty Island, the largest island in the Belcher Island archipelago of southeast Hudson Bay. For a detailed description of climate, vegetation, and geology of the Belchers see Chapter 2.

I established ten snow transects during summer 1990 in representative areas of six major range types (Chapter 2) within a 7 km distance from Sanikiluaq. Each transect consisted of 10 poles spaced at 10 m intervals. All poles were cut to a length of 2 m, clearly marked in 5 cm graduations, and placed such that the zero mark was at ground level. During the period 4 - 15 March 1991, I revisited each transect and measured integrated hardness with a Ramsonde penetrometer. Integrated Ram hardness is a measure of the total amount of work (kg-cm) required to push a cone shaped penetrometer from the top of the snow profile to ground level (see Skogland 1978). At each pole, I took two measures each of snow hardness and depth and recorded average values. This resulted in a sampling intensity of 10 measures at each transect.

Minimum sample sizes were based on variability of snow depth and hardness within a site (transect). I used the following equation (Krebs 1989, p. 177, Equation 5.4) to calculate sample sizes:

$$n = (170\ CV\ /r)^2$$

where: n = minimum sample size, r = desired relative error (20%), and CV = coefficient of variation (*i.e.* standard deviation / mean). Thus, by using this equation I calculated minimum sample sizes required to estimate the mean ($\pm$ 20%) at the 90% confidence level.

I used nested ANOVAs (Zar 1984) to determine whether there were significant differences in snow depth or hardness between range types or between transects within range types. I ommitted the "barren bedrock ridge" and "dwarf shrub gravel ridge" range types because I was only able to sample one transect in each of these communities (Table A-1). Data for snow depth and hardness were log transformed to satisfy the assumptions of analysis of variance (Zar 1984).

Results

Depth and integrated Ram hardness of snow in March on the Belcher Islands was highly variable. Variance (as indicated by the CV) was higher for estimates of snow hardness compared to snow depth. Minimum sample sizes varied accordingly (Table A-1). The coefficient of variation for both depth (CV = 1.08) and hardness (CV = 1.33) of snow was greatest at the site located in the barren bedrock ridges. Variation was lowest in sedge moss stream banks; the coefficient of variation was 0.31 and 0.46 for depth and hardness respectively. Consequently, required sampling intensity to estimate snow depth and hardness at a site was greatest in the barren bedrock ridge and least in sedge moss stream beds (Table A-1).

Range type and site, both had significant effects on snow depth (Table A-2a). With respect to integrated snow hardness, only site differences were significant (Table A-2b).

Discussion

To properly monitor snow conditions within range types on the Belcher Islands, permanent sites should be established in summer and revisited periodically during the winter months. Sampling intensity should be stratified according to range type and be reflective of microtopographic variability. In general, sites with a preponderance of large hummocks or ridges require greater sampling intensity than sites that are level or moderately undulating. A sampling intensity of 40 measures to estimate depth and hardness within a site should be considered for most range communities. In sedge moss stream beds sampling intensity may be reduced to 20 measures, whereas in barren bedrock ridges minimum sample size (n = 128) may be constrained by logistics.

This preliminary survey of snow conditions on the Belcher Islands showed that snow conditions were highly variable within and between range communities. The most probable reasons for the observed variability in snow conditions are twofold. Firstly, variability in microtopography increases variability in snow depth. Range communites were representive of vegetation and landscape conditions (Chapter 2). As a result, communities may be striated and dissected by rock or gravel ridges, hummocks, frost boils, or stream banks. Secondly, movement and redistribution of snow by wind influences depth and hardness of the snow pack. In arctic tundra where trees are absent, wind plays a critical role in the movement and redistribution of snow. Wind blown snow, or *upsik*, is a result of mechanical breakdown of snow crystals (Halfpenny and Ozanne 1990). Snow crystals are broken, redeposited, and densely packed by wind. Subsequently, these fragmented crystals sinter (freeze) together resulting in a snow pack that is more dense and harder than previous. Thus, in arctic tundra, hardness and depth of snow may vary relative to microtopographic characteristics of the habitat, predominant winds, and also the interaction of wind with macro-topographic features. This effect of wind and general topography on variability in depth and hardness of *upsik* was evident at site 'G' (Table A-1). This site was representative of the "mixed lichen-dwarf shrub flats" with respect to abundance and composition of vegetation. However, since this particular site was located on the leeward side of a large bedrock ridge, snow was excessively deep and hard. Therefore, *upsik* at site 'G' was atypical of the mixed lichen-dwarf shrub range type.

Table A-1. Mean depth and integrated ram hardness of snow in range communities on the Belcher Islands, March 1991.

Range Type[1]	Site	Mean Depth (cm)	Range	S.D.[2]	C.V[3]	Required Sample Size[4]	Mean Hardness[5]	Range	S.D.	C.V.	Required Sample Size
1	E	22	0-82	24	1.08	84	211	0-889	280	1.33	128
2	F	40	6-86	28	0.69	34	667	61-1205	427	0.64	30
3	D	29*	13-64	16	0.57	23	297*	44-738	208	0.70	35
	G	63**	20-124	32	0.51	19	1428**	99-3374	1071	0.75	41
	D & G	46ab	13-124	31	0.67	32	863	44-3374	949	1.10	87
4	A	37	13-47	12	0.32	7	444	116-842	238	0.54	21
	H	26	8-56	12	0.47	16	256	57-532	137	0.53	20
	A & H	31a	8-56	13	0.41	12	350	57-842	212	0.61	27
5	C	30	17-48	10	0.35	9	526	95-1086	316	0.60	26
	I	40	12-61	16	0.40	12	573	61-1347	426	0.74	40
	C & I	35a	12-61	14	0.40	12	550	61-1347	366	0.67	32
6	B	53	25-100	21	0.40	12	382	115-806	211	0.55	22
	J	56	36-77	13	0.23	4	667	367-893	185	0.28	6
	B & J	55b	25-100	17	0.31	7	525	115-893	242	0.46	15

[1] Range types are as follows: 1, Barren bedrock ridges; 2, Lichen dwarf shrub gravel ridges; 3, Mixed lichen-dwarf shrub flats; 4, Mixed lichen-dwarf shrub-sedge-moss hummocky meadows; 5, Dwarf shrub-sedge-moss hummocky meadows; 6, Sedge moss stream beds.

[2] Standard deviation

[3] Coefficient of variation (S.D./x)

[4] Required sample size to achieve a precision of $\pm$ 20% of the mean at 90% probability ($n = (170CV/20)^2$; Krebs 1989, p. 177).

[5] Integrated ram hardness (kg-f cm)[1]

Note: Significant differences ($p < 0.05$) between site means within a range community are indicated by asterices (*). Letters denote significant differences between mean values for range communities. See Table A-2 for associated ANOVA tables.

Table A-2.

a) Summary of nested ANOVA for snow depth (data were log transformed).

Source	Sum of Squares	df	*F*	p
Range type	0.69	3	6.07	0.001
Sites	0.80	4	5.19	0.001
Error	2.76	72		

b) Summary of nested ANOVA for integrated snow hardness (data were log transformed).

Source	Sum of Squares	df	*F*	p
Range type	0.66	3	1.83	0.150
Sites	2.25	4	5.19	0.002
Error	8.62	72		

Literature Cited

Adamczewski, J.Z., C.C. Gates, B.M. Soutar, and R.J. Hudson. 1988. Limiting effects of snow on seasonal habitat use and diet selection of caribou *(Rangifer tarandus groenlandicus)* on Coats Island, Northwest Territories. Canadian Journal of Zoology. 66: 1986-1990.

Brown, W.K., and J.B. Theberge. 1990. The effect of extreme snowcover on feeding-site selection in woodland caribou. Journal of Wildlife Management. 54: 161-168.

Collins, W.B., and T.S. Smith. 1991. Effects of wind-hardened snow on foraging by reindeer *(Rangifer tarandus)*. Arctic. 44: 217-222.

Halfpenny, J.C., and R.D. Ozanne. 1989. Winter: An Ecological Handbook. Johnson Publishing Co. Boulder, Colorado, USA.

Krebs, C.J. 1989. Ecological Methodology. Harper Collins, New York, New York, USA.

Laperriere, A.J., and P.C. Lent. 1977. Caribou feeding sites in relation to snow characteristics in northeastern Alaska. Arctic. 30: 101-108.

Ouellet, J.P. 1992. Ecology on an introduced caribou population on Southampton Island, N.W.T., Canada. Ph.D. Thesis. University of Alberta. Edmonton, AB. 123 pp.

Pruitt, W.O. 1959. Snow as a factor in the winter ecology of barren-ground caribou *(Rangifer arcticus)*. Arctic. 12: 158-179.

Pruitt, W.O. 1979. A numerical "Snow Index" for reindeer *(Rangifer tarandus)* winter ecology (Mammalia, Cervidae). Ann. Zoologica Fennici. 16: 271-280.

Skogland, T. 1978. Characteristics of the snow cover and its relationship to wild mountain reindeer *(Rangifer tarandus tarandus* L.) feeding strategies. Arctic and Alpine Research. 10: 569-580.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc. Inglewood Cliffs, New Jersey, USA.